# The Thick-billed Murres of Prince Leopold Island

A.J. Gaston and D.N. Nettleship

Environment Canada
Canadian Wildlife Service

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*Front cover*:
Thick-billed Murres on breeding sites on Prince Leopold Island, NWT, 1 August 1975 (D.N. Nettleship).

*Back cover*:
Thick-billed Murres and their terrestrial and marine habitats, Prince Leopold Island, 1 August 1975 (D.N. Nettleship).

*Frontispiece*:
Thick-billed Murre incubating, Prince Leopold Island.
Original acrylic painting by Barbara Dodge.

# The Thick-billed Murres of Prince Leopold Island

## A study of the breeding ecology of a colonial high arctic seabird

by A.J. Gaston and D.N. Nettleship

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## Dedication

We dedicate this work with gratitude and thanks to

**Hugh Boyd**, who initiated and established the seabird program within the Canadian Wildlife Service and provided continual support and encouragement through the years and

**Leslie M. Tuck**, who pioneered the study of the Thick-billed Murre in Arctic Canada including Lancaster Sound.

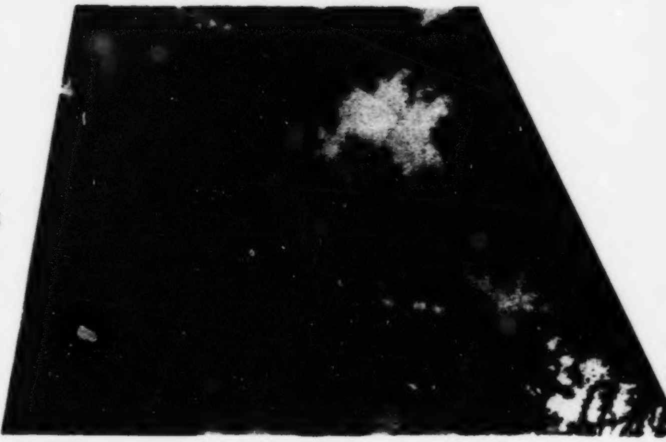
## The authors

**Tony Gaston**, born in 1946 in Croydon, England, has been a birdwatcher for most of his life. He read natural sciences and physica anthropology at Clare College, Cambridge (1964–67) and then spent 3 years as an itinerant birdwatcher and fossil collector in Africa and Asia, hitch-hiking across the Sahara in the process. From 1970 to 197 he studied co-operative breeding in Indian birds for a Ph.D. at the Edward Grey Institute of Field Ornithology, Oxford University. In th summers of 1975–77 he carried out research for the Canadian Wildlif Service (CWS) on Thick-billed Murres at Prince Leopold Island. From 1977 to 1978 he was Commonwealth Fellow at the University of Calicut, India, and from November 1978 to June 1980 led a project to investigate the status of wildlife in the western Himalayas. Since June 1979 he has been a research scientist with CWS, in charge of co-ordinating research on seabirds. Tony is married to Anne-Marie (Anjali), the well-known East Indian classical dancer.

**David N. Nettleship** studied biology at Sir George Williams University in Montreal (B.Sc.) and the University of Saskatchewan i Saskatoon (M.Sc.) and zoology at McGill University in Montreal (Ph.D.). He was a Research Fellow at the Edward Grey Institute of Field Ornithology, Oxford University. In 1971 he joined the Canadian Wildlife Service after a lengthy informal association dating back to 1965 and now lives in Nova Scotia and works at the Bedford Institute of Oceanography where he heads a long-term research program on the reproductive ecology of seabird populations in eastern Canada. Nettleship's researches into the life histories and breeding regimes of seabirds and shorebirds have taken him to the northernmost regions of land including northern Ellesmere Island and Pearyland, Greenland and throughout the other islands and mainland regions of Arctic Canada. His main research interest is animal ecology and behaviour, particularly that of colonial seabirds and the auk family. He is a member of many scientific societies, and served for several years as Co-Chairman on the Canadian Committee for the International Biological Programme Conservation Terrestrial — Panel 9. He is still deeply involved in establishing land-use policy and protection for biologicall important sites in Canada and is also active in the making of educational films on the conservation of marine fauna and its habitats. His other books are *Atlas of Eastern Canadian Seabirds* (1975), *Ecologica Sites in Northern Canada* (1975), and *Conservation of Marine Birds of Northern North America* (1979).

The following series of plates depicts the Thick-billed Murre, its biology and environment through the year, from late winter to the onset of the following winter.

**Plate 1.**
The study area.
*Above*, the Lancaster Sound region as seen from a satellite (mosaic prepared by Canada Centre for Remote Sensing and the National Air Photo Library using LANDSAT images recorded during the summer, 1973–77); *below*, aerial view of Prince Leopold Island from the northeast, 7 July 1977 (D.N. Nettleship).



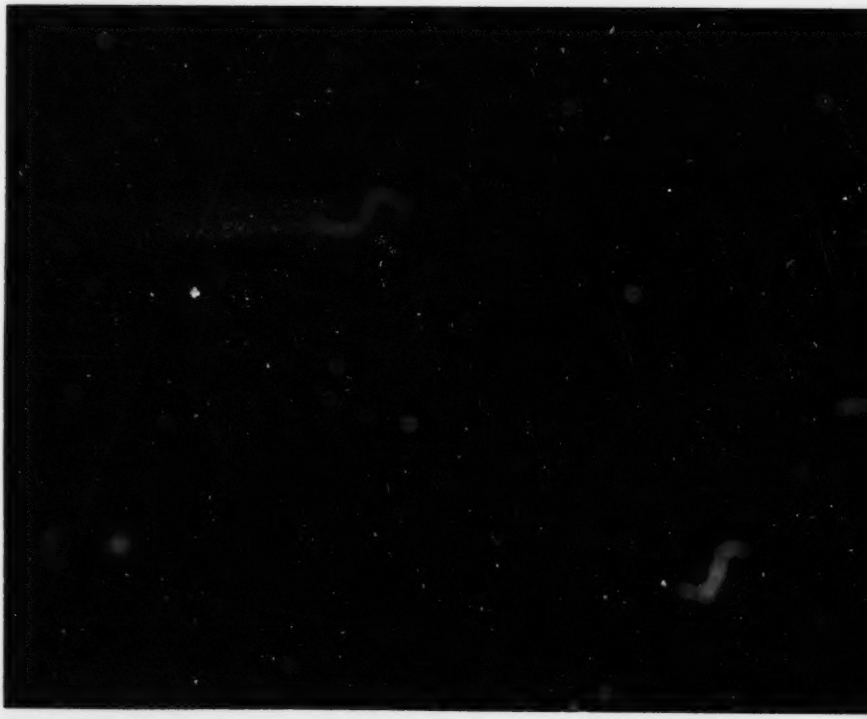


**Plate 2.**
Cliffs and beaches of Prince Leopold Island. *Above*, the cliffs along the north coast, 16 August 1977 (F. Bruemmer); *below*, gravel beach of the south spit and south cliffs showing extensive scree slopes, 23 June 1975 (D.N. Nettleship).

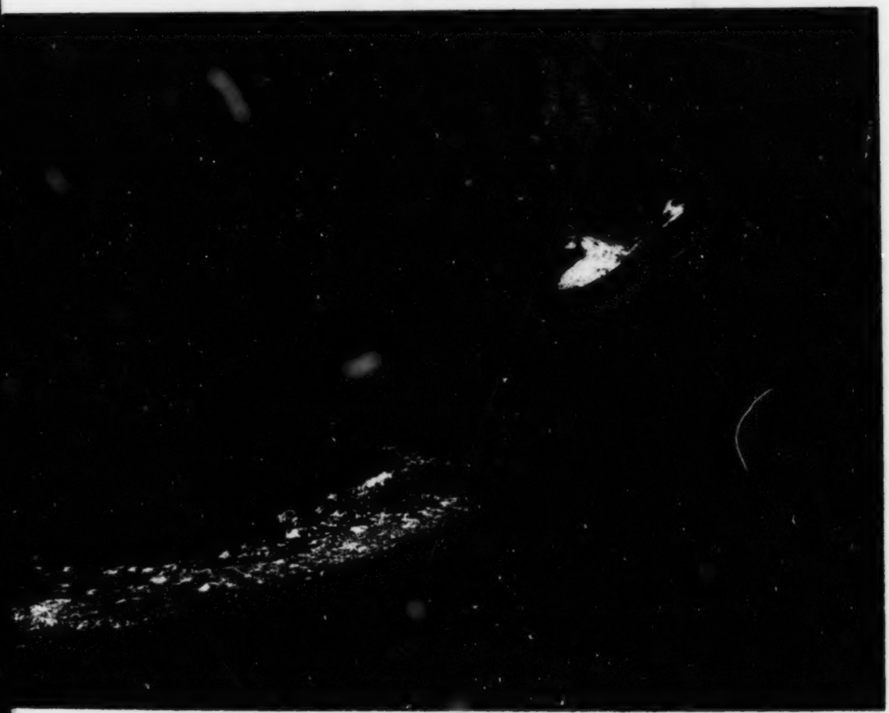


**Plate 3.**
Late winter conditions at Prince Leopold Island.
*Above*, snow cover on 18 May 1976 as viewed from the cliff top near camp looking towards Cape Admiral McClintock (D.N. Nettleship);
*below*, at the camp site, 24 May 1976 (D.N. Nettleship).

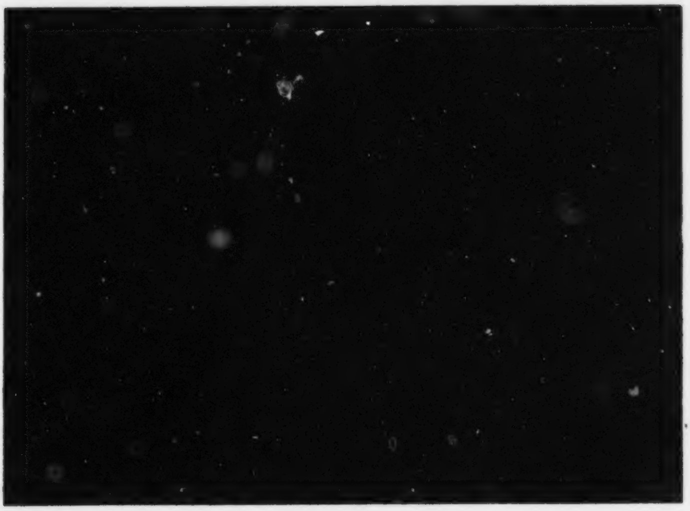
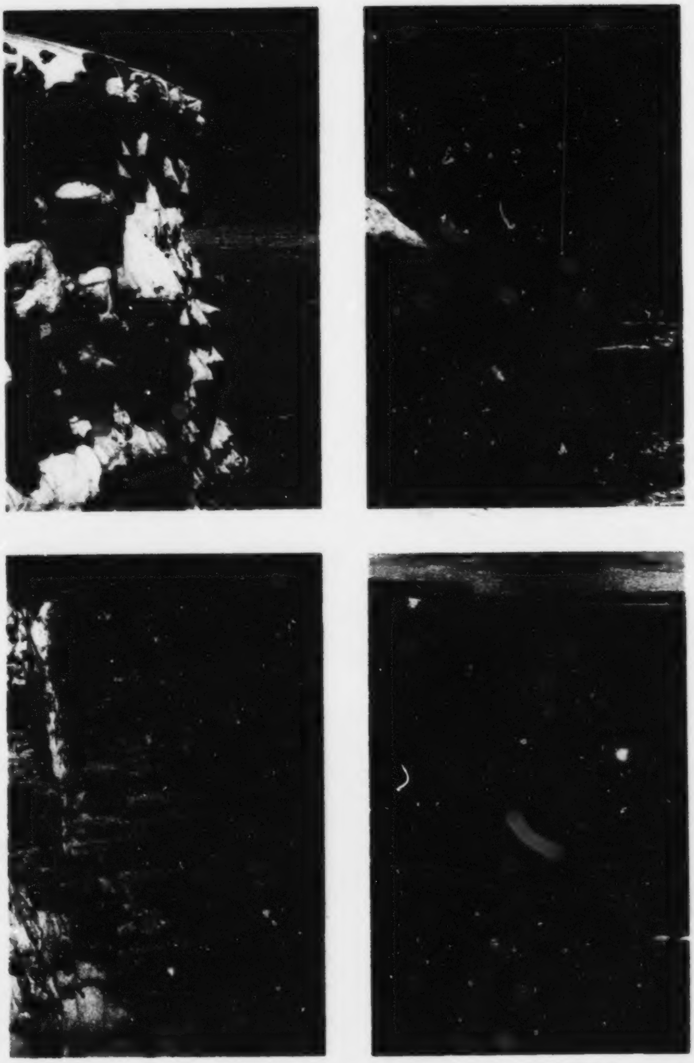


**Plate 4.**
Snow conditions on the cliffs soon after the arrival of Thick-billed Murres in spring, at the start of egg-laying. *Above left*, the cliffs and landfast sea-ice near camp looking southeast on 18 May 1976 (D.N. Nettleship); *above right*, the same area on 4 June 1977 (D.N. Nettleship); *below left*, the massive cliffs at area G on 22 May 1976 (D.N. Nettleship); *below right*, the same cliffs on 24 June 1975 (D.N. Nettleship).



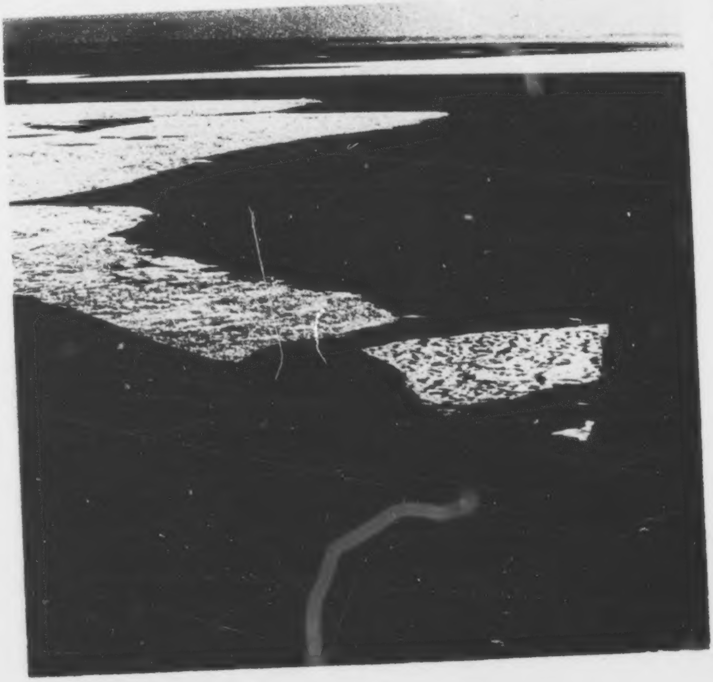


**Plate 5.**
(*Opposite page*)
Snow cover
on the south spit.
*Above*, near the base
of the spit looking
east on 19 June 1977
(D.N. Nettleship);
*below*, the same
general area of the
spit looking north on
8 July 1977
(D.N. Nettleship).

**Plate 6.** (*This page*)
Spring and early
summer.
*Above*, sea cliffs
and gravel beach on
the south coast,
24 June 1977
(D.N. Nettleship);
*below*, snow-free
slope facing
southeast,
with *Saxifraga
oppositifolia*
in flower, near area S,
24 June 1975
(D.N. Nettleship).

**Plate 7.** Prince Leopold Island's breeding seabirds. *Above left*, Northern Fulmar (E. Greene); *above right*, Black-legged Kittiwake (F. Bruemmer); *centre*, Glaucous Gull (F. Bruemmer); *below*, Black Guillemot (E. Greene); *opposite page*, Thick-billed Murre (E. Greene).

XV

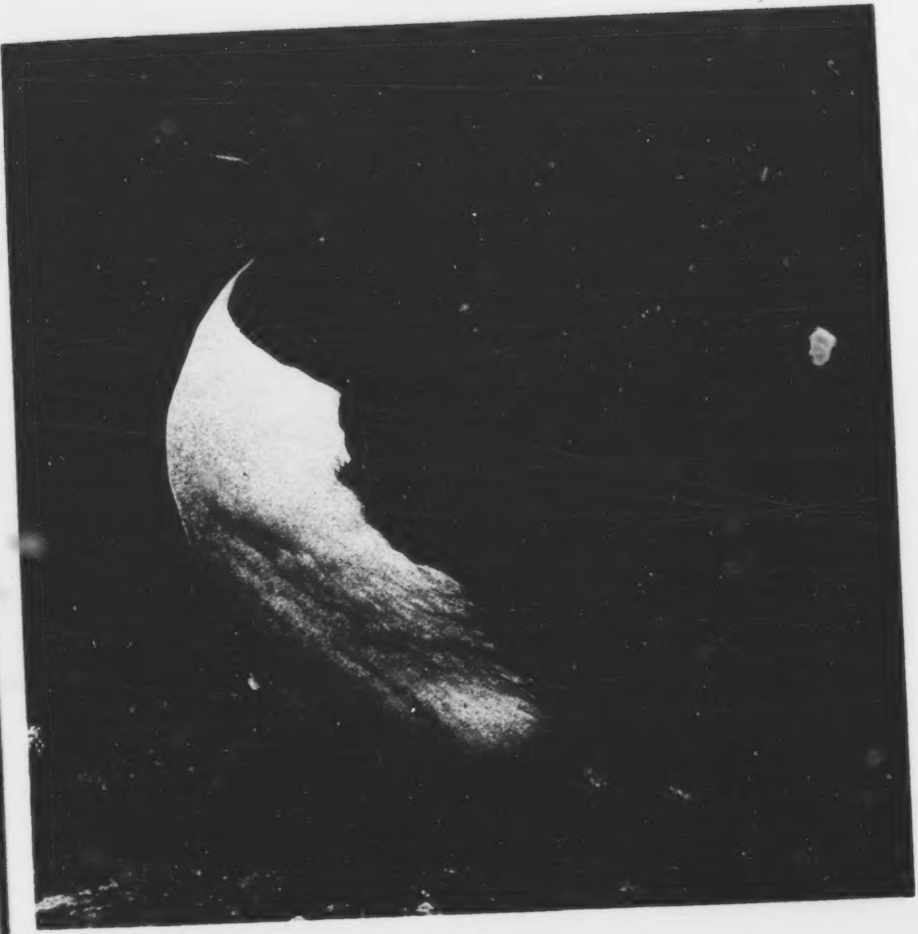


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**Plate 8.** (*Opposite page*)
Ice-edges.
*Above*, ice-edge
extending from the tip
of the south spit of
Prince Leopold Island
southwest to Cape Clarence,
Somerset Island,
5 June 1977
(D.N. Nettleship);
*below*, Thick-billed Murres
feeding along the
Wellington Channel
ice-edge, late June 1977
(K.J. Finley, courtesy of
Polar Gas).

**Plate 9.** (*This page*)
Thick-billed Murre
breeding areas.
*Left*, cliffs at areas G
and H, 7 July 1977
(D.N. Nettleship);
*above right*, cliffs
at areas F and G
viewed from top of H,
24 June 1975
(D.N. Nettleship);
*below right*, southeast
bird cliffs as seen
from study plot S,
1 August 1975
(D.N. Nettleship).

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**Plate 10.**
High-density breeding of Thick-billed Murres at Prince Leopold Island.
*Above*, cliffs near area G, 28 August 1978 (E. Greene);
*below*, top of precipitous rock stack at area G, mid August 1977 (F. Bruemmer).

**Plate 11.**
Typical Thick-billed Murre breeding sites at Prince Leopold Island.
*Above*, narrow ledges high up on the cliffs, mid August 1977 (F. Bruemmer); *below*, close-up view showing average bird density and the unstable condition of the ledges, 1 August 1975 (D.N. Nettleship).

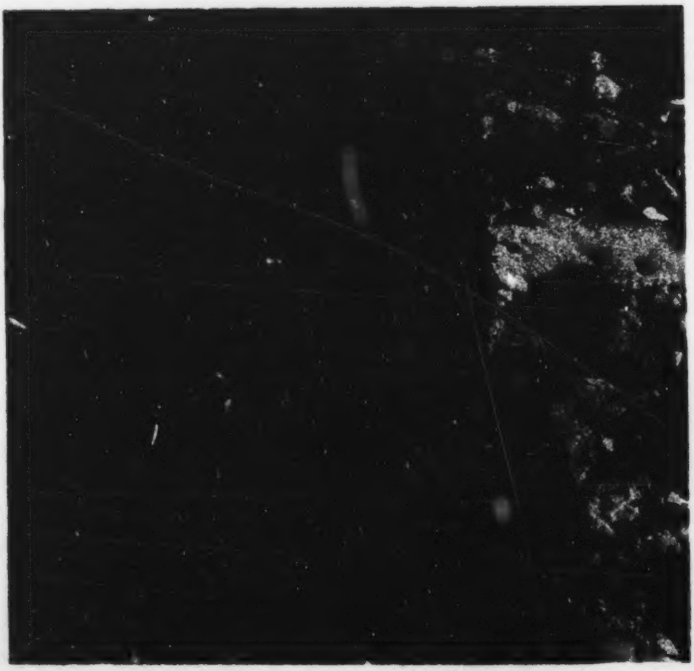

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**Plate 12.**
Linear ledge breeding habitat of Thick-billed Murres at study plot S. *Above*, horizontal lines of breeding birds on narrow rock ledges along the sheer cliff-face, 1 August 1975 (D.N. Nettleship) — the observation blind at study plot S1 is visible; *below*, close-up view of distribution of the birds, 1 August 1975 (D.N. Nettleship).

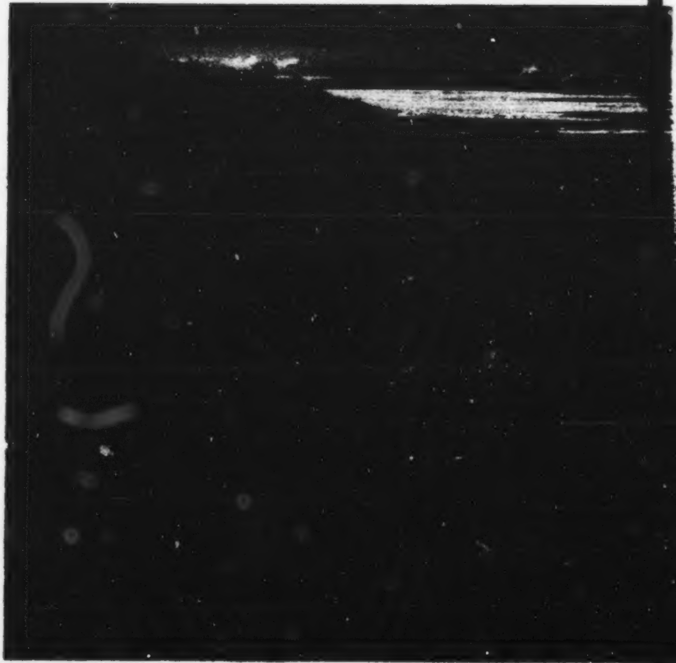
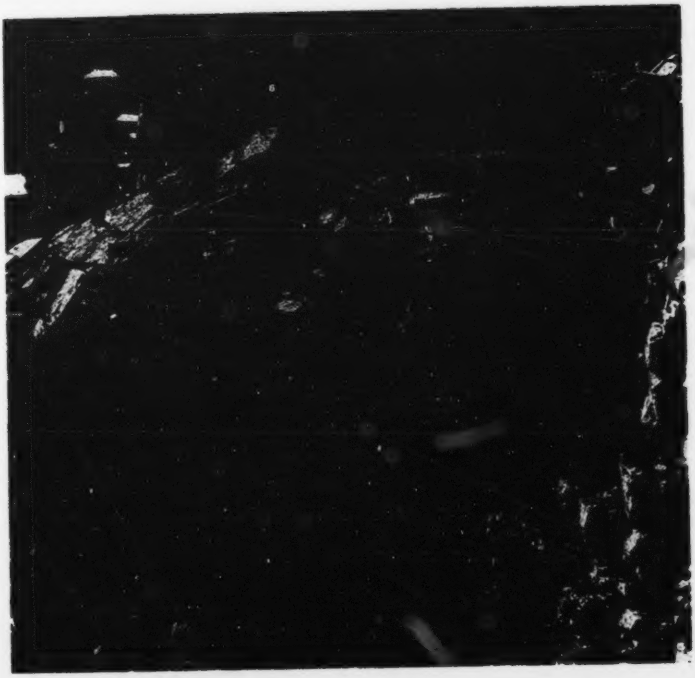


**Plate 13.**
Thick-billed Murre study plot S1 on 27 June 1975. *Above*, birds as seen from the observation blind (D.N. Nettleship); *below*, close-up of a portion of the study plot (D.N. Nettleship).



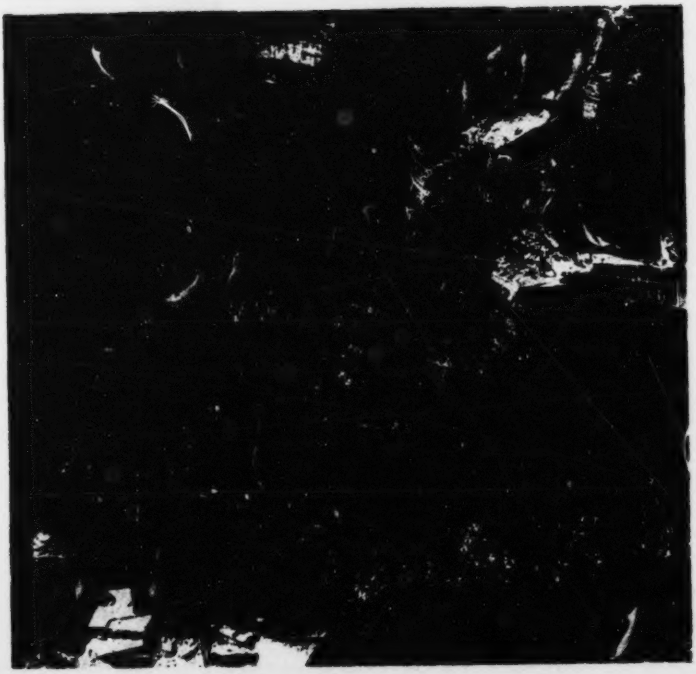


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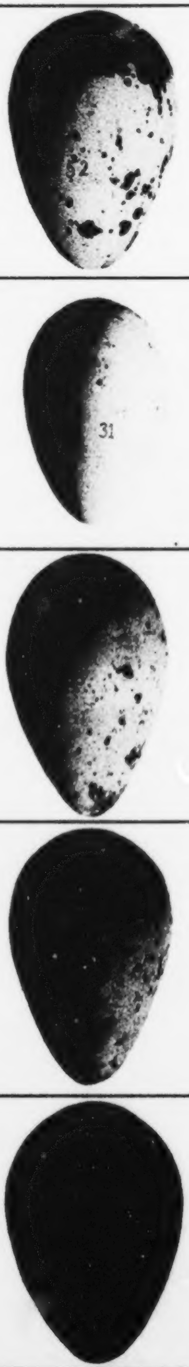
**Plate 14.**
Variation in the ground colour density among the eggs of Thick-billed Murres at Prince Leopold Island.
From the top:
Class 1,
Class 2,
Class 3,
Class 4,
Class 5
(see Chapter IV, section 2 for further details).



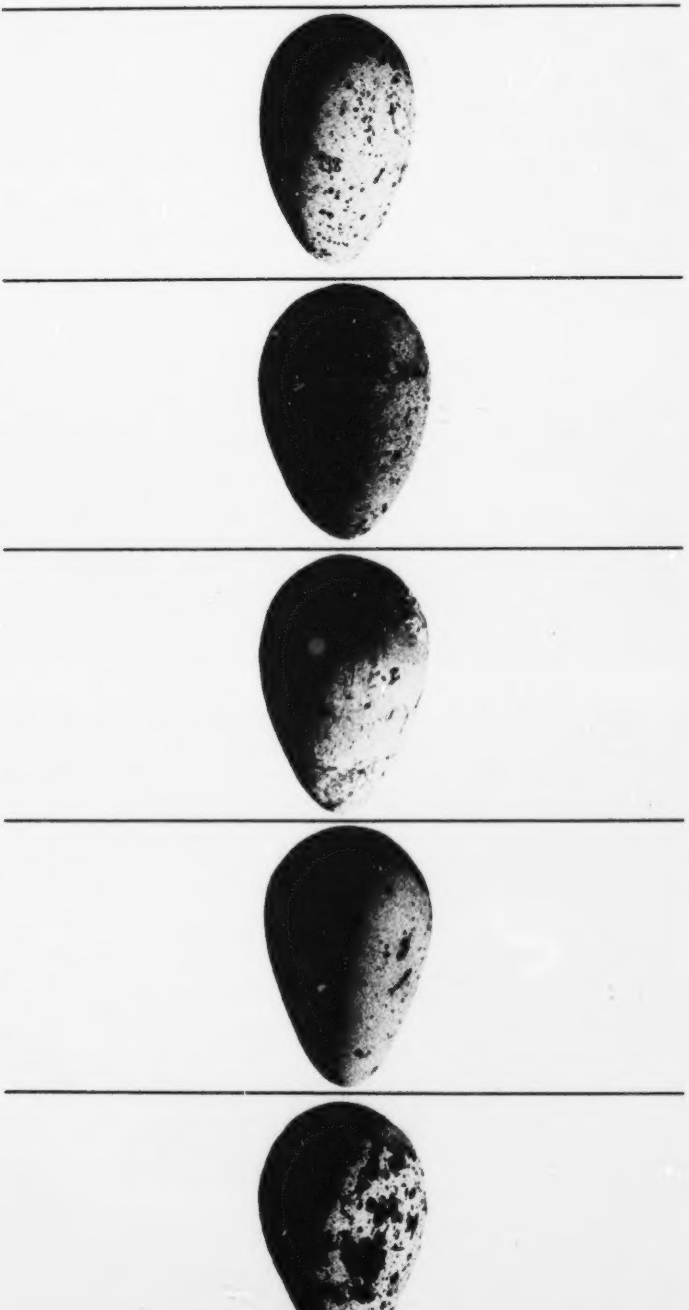


**Plate 15.** Variation in size and colour of markings among the eggs of Thick-billed Murres at Prince Leopold Island. From the top: black speckles with blotches at large end; brown spots with a few scribbles; faint brown scribbles; black scribbles; black blotches.

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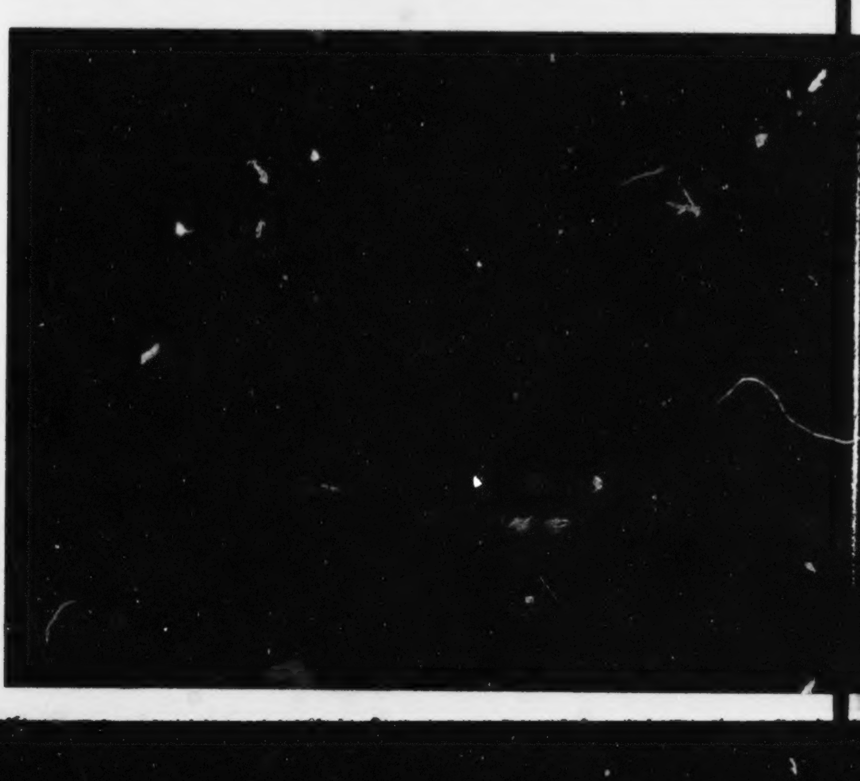
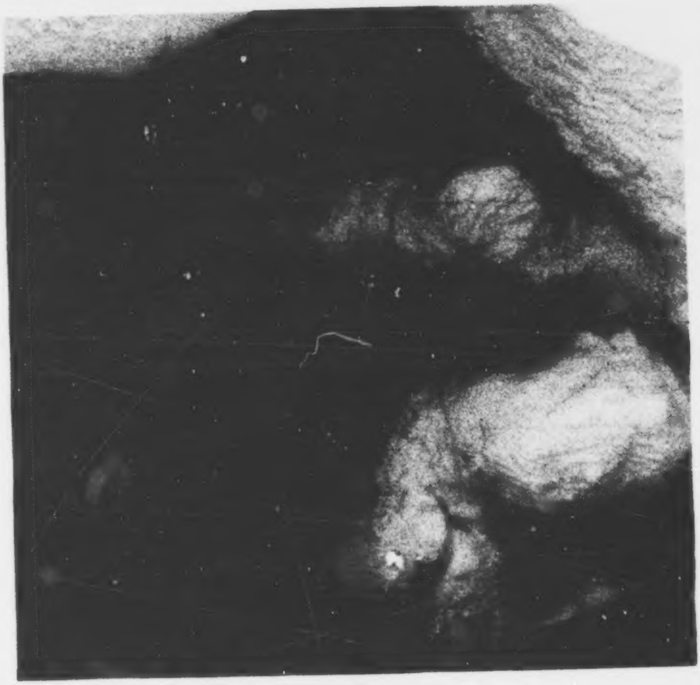


**Plate 16.**
(*Opposite page*)
Thick-billed Murres at sea.
*Above*, a group on the water near Prince Leopold Island, 20 July 1977 (E. Greene);
*below*, close-up of single bird, 20 July 1977.

**Plate 17.**
(*This page*)
Delivery of food to Thick-billed Murre chicks at the colony.
*Above*, chick meal of one sculpin *Triglops* sp., 19 August 1978 (E. Greene);
*below*, adult murre holding a sculpin, 17 August 1978 (E. Greene).

**Plate 18.**
(*Opposite page*)
Thick-billed Murre chicks at the colony. *Above*, 3-day-old chick, 17 August 1978 (E. Greene); *below*, two ≃ 20-day-old chicks showing the different chick plumage types — on the left, summer form with dark throat and cheeks and on the right, winter form with white neck and cheeks, 16 August 1977 (E. Greene). (See Chapter IV, section 3.2, for further details.)

**Plate 19.**
(*This page*)
The start of winter and the penalty for late laying. *Above*, breeding ledges at study plot U covered with thick, compacted hard snow, 7 September 1977 (D.N. Nettleship); *below*, close-up of two late breeders, each brooding a chick on study plot U, 7 September 1977 (D.N. Nettleship).



# Contents

5 **List of tables**
10 **List of figures**
18 **List of appendices**
20 **Foreword**
21 **Preface**
24 **Résumé**
25 **Acknowledgements**

**Chapter I: Introduction**

28 **1. Background information**
30 **2. Study area**
30 2.1. Location and description
30 2.2. History
33 2.3. Seabird populations
34 2.4. Flora and other fauna
36 **3. Physical environment**
36 3.1. Summer climate
39 3.2. Currents
39 3.3. Ice conditions
39 3.4. Structure of the breeding cliffs
42 **4. Study techniques**

**Chapter II: Attendance and behaviour at the colony**

46 **1. Introduction and methods**
47 1.1. Colony attendance
47 1.2. Behaviour
49 **2. Descriptions of behaviour patterns**
49 2.1. Arrival
50 2.2. Copulation
50 2.3. Aggression
51 2.4. Departure
52 2.5. Behaviour on the water

53 **3. Colony attendance**
53 3.1. Pre-laying period
57 3.2. Incubation and chick-rearing periods
61 3.3. Diurnal variation in attendance
64 3.4. Attendance patterns and population monitoring
68 **4. Behaviour**
68 4.1. Behaviour during the pre-laying period
72 4.2. Egg laying and incubation
77 4.3. Chick-rearing period
81 4.4. Behaviour of prospectors
86 4.5. Role of prospectors in determining fluctuations in attendance
91 4.6. Aggression during incubation and chick rearing
97 4.7. Factors determining seasonal changes in patterns of behaviour
98 4.8. Behaviour at fledging
102 4.9. Role of the sexes in the breeding cycle
103 4.10. Predation and anti-predator behaviour
106 **5. Census and population size**
106 5.1. Methods
107 5.2. Results
110 **6. Summary**

**Chapter III: Timing and success of reproduction**

114 **1. Introduction and methods**
114 1.1. Methods and variables measured
117 1.2. Discussion of methodology
123 **2. Timing of breeding**
123 2.1. Egg laying
126 2.2. Hatching and length of incubation period
131 2.3. Fledging and the duration of the chick-rearing period
133 2.4. Factors influencing timing of breeding
138 **3. Breeding performance**
138 3.1. Hatching success
141 3.2. Fledging success
141 3.3. Breeding success
144 3.4. Inter-plot comparisons

145 **4. Factors affecting breeding success**
145 4.1. Persistence of site occupancy from year to year
147 4.2. Characteristics of the breeding site
156 4.3. Combined effects of breeding-site characters
161 4.4. Discussion of breeding success
166 **5. Summary**

**Chapter IV: Development of young**

168 **1. Introduction**
169 **2. The egg**
169 2.1. Methods
169 2.2. Egg weight and volume
170 2.3. Egg colour
171 2.4. Discussion
174 **3. Chick growth**
174 3.1. Methods
174 3.2. Plumage development
175 3.3. Weight
181 3.4. Maternal influence
186 3.5. Effects of weather
186 3.6. Discussion
191 **4. Feeding rates and chick diet**
191 4.1. Methods
193 4.2. Feeding rates
199 4.3. Feeding rates and foraging ranges
201 4.4. Chick diet
205 4.5. Food consumption by chicks
206 4.6. Discussion
208 **5. Summary**

Chapter V: Adult weight, food, and feeding areas

210 **1. Introduction**
211 **2. Measurements and condition**
211 2.1. Methods
211 2.2. Measurements
212 2.3. Condition of gonads
212 2.4. Brood patches
213 2.5. Weight and body condition
218 **3. Adult diet**
218 3.1. Methods
218 3.2. Results
220 3.3. Interpretation of adult diets
227 **4. Feeding areas**
227 4.1. Methods
228 4.2. Results of aerial surveys
234 4.3. Habitat preference
237 4.4. Estimates of total numbers of birds at sea
238 4.5. Foraging range
239 4.6. Observations on directions of arrival and departure at the colony
243 4.7. The location of feeding areas by foraging murres
246 **5. Summary**

Chapter VI: Conclusions and general considerations

248 **1. The Thick-billed Murre and the seabird community**
255 **2. Causes and consequences of coloniality in the Thick-billed Murre**
260 **3. Factors controlling population size**
267 **4. The fledging strategy of the Thick-billed Murre**
269 **5. The structure of the colony**
272 **6. Summary**

273 **References**
285 **Appendices**

## List of tables

29 Table 1. Thick-billed Murre colonies and populations in the western Atlantic

33 Table 2. Populations and general breeding distributions of seabirds at Prince Leopold Island, 1975–77

59 Table 3. Comparison of some important attendance statistics 1975–77

59 Table 4. Differences between mean counts of birds made at seven plots from 1–8 August in 1976 and 1977

61 Table 5. The effect of visibility on “d” in 1977

61 Table 6. Correlation between mean counts of birds at plot S1 during watches every 3 days, 25 July – 21 August 1977 inclusive, and wind speed and visibility

66 Table 7. Comparison of standard errors calculated for the difference between mean counts over two periods in 1976 and 1977 and the standard errors calculated for mean differences between paired observations on the same dates

70 Table 8. Sex of birds involved in copulations or attempted copulations immediately after landing, in relation to time of day during the pre-laying period in 1975

75 Table 9. Incidence of “butterfly flight” in relation to whether birds subsequently landed on the sea or not

75 Table 10. Attendance of marked pairs during the interval between the removal of their egg to re-laying and after re-laying at plot U in 1977

78 Table 11. The numbers of fish delivered to chicks at plot U by male and female parents on 24 and 27 August 1977

78 Table 12. Numbers of fish brought by individual birds between incubation exchanges at plot U on 24 and 27 August 1977

78 Table 13. Time spent between arrival and exchange of brooding duty after chicks had been fed, in relation to date and the age of the chicks in 1976 and 1977

80 Table 14. Behaviour of birds leaving their site after their chick had been fed, in relation to whether or not there had been an incubation exchange

93 Table 15. Frequency of fighting at sites where chicks hatched in relation to the date of hatching at plot S1 between 25 July and 18 August 1977

93 Table 16. Frequency of fighting at sites in relation to the number of neighbours at plot S1 between 25 July and 18 August 1977

93 Table 17. Incidence of fighting at sites in relation to the presence of eggs or chicks at plot S1 in 1977

| | |
|---|---|
| 93 | Table 18. Incidence of fighting at sites in relation to whether a chick was present, had fledged, or disappeared prematurely, at plot S1 in 1977 |
| 105 | Table 19. Number of eggshells of Thick-billed Murres collected at nest-sites of three pairs of Glaucous Gulls located at the top of the cliffs during 1975 |
| 107 | Table 20. Comparisons of direct and photographic counts made on 9 August 1975 at Prince Leopold Island |
| 108 | Table 21. Comparison of the results of direct counts made on the area of cliffs between E and I in 1975–77 |
| 108 | Table 22. Comparison of a preliminary analysis of population made in 1975 using limited information and a detailed census performed in 1976 and 1977 |
| 121 | Table 23. Comparison of observed dates of laying with those estimated from observed dates of hatching for plot S1 in 1976 |
| 125 | Table 24. Correlation coefficients for the dates of laying at the same site in different years |
| 130 | Table 25. Median dates of hatching at seven study plots in 1975, 1976, and 1977 |
| 130 | Table 26. Correlation coefficients for the date of hatching at the same site in different years |
| 130 | Table 27. Comparison of numbers of sites at plot S1 where chicks hatched early in 1, 2, or 3 seasons with expected frequencies based on the null hypothesis that dates of hatching at particular sites are independent between years |
| 138 | Table 28. Numbers of eggs laid, hatched, and fledged on seven study plots in 1975–77 |
| 139 | Table 29. Causes of egg mortality observed at study plot S1 in 1975 and 1977 |
| 141 | Table 30. Proportion of lost eggs that were replaced in relation to the date of laying of the first egg |
| 142 | Table 31. Hatching, fledging, and breeding success at seven study plots in 1975–77 |
| 143 | Table 32. Comparisons of breeding success at the same site in different years |
| 146 | Table 33. Success of first eggs at sites not occupied in either of 1976 and 1977, compared with success at sites occupied in both years |
| 146 | Table 34. Persistence of site occupancy between 1976 and 1977 in relation to breeding success in 1976 |
| 146 | Table 35. Dates of hatching at plot S1 in 1977 in relation to occupancy and breeding success in 1976 |
| 152 | Table 36. Breeding success of all sites in relation to the number of neighbours |

152 Table 37. Breeding success at all sites in relation to the slope of the ledge

152 Table 38. Breeding success in relation to the width of the ledge

152 Table 39. Breeding success in relation to the number of walls

154 Table 40. Breeding success in relation to the presence or absence of a crack in which the chick can hide

154 Table 41. Breeding success in relation to the extent to which sites were roofed

154 Table 42. Breeding success in all three seasons in relation to the timing of disappearance of snow from breeding sites in 1976

156 Table 43. Timing of laying of first eggs on study plot S1 in 1977 in relation to the date of disappearance of snow from the site

157 Table 44. Breeding success in relation to the number of neighbours, controlling for walls, width, and slope

157 Table 45. Breeding success in relation to the number of walls, controlling for width and slope

157 Table 46. Breeding success in relation to width, controlling for slope

159 Table 47. Index of predicted breeding success for seven study plots compared with observed breeding success

160 Table 48. Mean dates of hatching in 1977, broken down by neighbour, wall, and slope categories

162 Table 49. Proportions of chicks hatching early in five zones on plot S1

163 Table 50. Estimation of the potential reduction in adult survival during the subsequent year caused by late breeding

165 Table 51. Estimate of post-fledging mortality occurring between fledging and arrival on the wintering grounds off Newfoundland

170 Table 52. Volume indices for eggs

170 Table 53. Egg markings in relation to ground colour

171 Table 54. Distribution of ground colour classes at three different areas of the east cliffs in 1977

175 Table 55. Proportion of chicks on two plots with "summer" and "winter" plumage in 1977

177 Table 56. Inter-year comparisons for chick growth characteristics

181 Table 57. Inter-plot comparisons for chicks weighed on plots at E and S in 1977

185 Table 58. Correlation matrix for growth characteristics of chicks on study plots at S in 1977

| | |
|---|---|
| 185 | Table 59. Correlation matrix for growth characteristics of chicks on study plots at E in 1977 |
| 185 | Table 60. Summary of correlations among growth parameters of chicks on study plots S and E in relation to predictions for all years |
| 186 | Table 61. Comparison of the weight change observed for chicks during their last 2 days before fledging with the change in weight of chicks at the same age which fledged later, on study plots at G and S combined for 1977 |
| 194 | Table 62. Distribution of numbers of meals delivered to chicks during the first five 4-h watches after hatching in 1977 |
| 195 | Table 63. Proportion of chicks fed at above the median rate on three areas of study plot S1 |
| 198 | Table 64. Comparison of feeding rates on 21 August 1977 between chicks that fledged during the next 48 h and those over 16 days old that did not fledge until later |
| 201 | Table 65. Calculation of estimates of the time spent by breeding murres foraging for themselves and for their chicks in late July and early August 1976 |
| 202 | Table 66. Numbers of individual food items recorded in the diet of Thick-billed Murre chicks at Prince Leopold Island, 1975–77 |
| 202 | Table 67. Proportion of fish other than *Boreogadus* delivered to chicks, according to the method of collection |
| 202 | Table 68. Size classes of fish delivered to murre chicks, according to age of chick and method of collection |
| 204 | Table 69. Estimated sizes of fish delivered to chicks during watches in late August, 1976 and 1977 |
| 204 | Table 70. Estimated sizes of fish delivered to chicks on 31 August 1976, in relation to the number of times that the chicks were fed during a 12-h watch |
| 205 | Table 71. Calculations of total food intake by murre chicks and conversion ratio |
| 212 | Table 72. Measurements of birds collected at Prince Leopold Island during 1975–77 |
| 216 | Table 73. Amounts of subcutaneous fat observed on specimens collected at three different periods |
| 216 | Table 74. Inter-year differences in the distribution of fat classes for birds collected in June and August at Prince Leopold Island |
| 216 | Table 75. Mean weights of two samples of adult Thick-billed Murres collected in Lancaster Sound in August 1976 |
| 218 | Table 76. Proportions of stomachs containing food remains among Thick-billed Murres collected in 1975–77 |

219 Table 77. Frequency of different taxa in the digestive tracts of Thick-billed Murres collected at Prince Leopold Island, calculated as percentages on the number of tracts containing food remains

231 Table 78. Numbers and densities of Thick-billed Murres on coastal, off-shore, and ice-edge transects, and proportion of 2-min periods in which they were recorded on each of three surveys during 1977

235 Table 79. Comparison of densities of Thick-billed Murres recorded on coastal and off-shore transects prior to the major fall exodus during 1976 and 1977

237 Table 80. Estimates of the total numbers of Thick-billed Murres in survey area based on densities recorded within the transects

241 Table 81. Sizes of flocks and rates of departure of Thick-billed Murres recorded leaving the tip of the south spit on 6 days in 1977

244 Table 82. Hypothetical calculations of the volume and density of murre "traffic" inbound from feeding area x

249 Table 83. Census figures for seabird species breeding in the Lancaster Sound area and for Prince Leopold Island alone

249 Table 84. Indices of species diversity for selected seabird communities in the Atlantic and northern Pacific oceans

250 Table 85. Volume of water potentially available for foraging to species breeding on Prince Leopold Island during the chick-rearing period

253 Table 86. Generalized comparison of food brought to seabird chicks at Prince Leopold Island during July–August

256 Table 87. Sizes of murre colonies in the western Atlantic and eastern Canadian Arctic, in relation to the frequency of drifting pack-ice during the chick-rearing period

## List of figures

| | |
|---|---|
| 31 | Figure 1. Lancaster Sound and vicinity |
| 32 | Figure 2. Prince Leopold Island, Northwest Territories |
| 34 | Figure 3. Sketch map of Prince Leopold Island showing physiographic features, location of research camp and East Cliff colony study area, and the general breeding distribution of Northern Fulmars and Thick-billed Murres |
| 37 | Figure 4. Some climatic conditions recorded during the breeding season at Prince Leopold Island, 1975–77 |
| 38 | Figure 5. General pattern of surface currents in Barrow Strait – Lancaster Sound |
| 40 | Figure 6. Inter-year differences in the positions of ice edges in the Barrow Strait – Lancaster Sound area, 1975–77 |
| 41 | Figure 7. Thick-billed Murres on section of East Cliff colony showing density of breeding birds and characteristics of the frost-fractured and horizontal cleavage of the rock-ledge habitat |
| 43 | Figure 8. Locations of major headlands and general study areas along the East Cliff colony |
| 54 | Figure 9. Daily counts of birds on study plots made between 1700 and 1900 h during the pre-laying period in 1975–77 |
| 55 | Figure 10. Counts of birds made from a time-lapse cine film showing the build-up in numbers at plot S1 between 1700 h 1 June to 0900 h 2 June 1976 |
| 55 | Figure 11. Comparison of counts of birds made on the study plots with those made on a much larger area at G during the pre-laying period in 1976 |
| 56 | Figure 12. A comparison of changes in numbers of birds on the East Cliff and North Spit study plots over a 48-h period, June 1977 |
| 58 | Figure 13. Daily counts of birds at all plots on Prince Leopold Island in 1976 and 1977 smoothed as 7-day running means and 7-day means derived from counts made by Tuck (1961) in 1957 at Cape Hay, Bylot Island |
| 60 | Figure 14. A comparison of the seasonal variation in counts of birds at plots Q1 and Q4, both on the same cliff and only about 80 m apart |
| 60 | Figure 15. The relationship of sample size to coefficient of variation for counts of birds made during 1–8 August 1977 |
| 62 | Figure 16. Counts of birds made every 2 h at all plots and at S1 only on 11 and 29 July 1976 |
| 63 | Figure 17. Means of counts of birds made every 2 h on six watches during the incubation period and five watches during the chick-rearing period at plot S1 in 1975 |

63 Figure 18. Coefficients of variation for counts of birds made every 2 h over a 24-h period on 11 watches at plot S1 during 1975

64 Figure 19. Numbers of birds present on plot S1 during the last four 24-h watches in 1975

66 Figure 20. Relationship between the number of days of replicate counts and the standard error of the mean, beginning from 1 July and 1 August 1977

68 Figure 21. Rates of copulation and attempted copulation observed during the pre-laying and early incubation periods

69 Figure 22. Rates of copulation observed at plot G3 in 1975 in relation to the number of birds present on the nearby plots G1 and G4

71 Figure 23. Frequency of fighting during the pre-laying periods in 1975 and 1976

71 Figure 24. Frequency of fighting in relation to the number of birds arriving on plot G3 during pre-laying in 1975

72 Figure 25. Number of incubation changes observed in 24 h in relation to the time elapsed since egg laying at plot S1 on 2 July 1975

73 Figure 26. Number of incubation exchanges observed during 24-h watches in relation to date at plot S1 in 1975 and 1977

73 Figure 27. Time intervals between arrivals and incubation change-overs at plot S1, 22–31 July 1977

74 Figure 28. Median duration of time interval between arrival and exchange in relation to date at plot S1 in 1977

76 Figure 29. Incubation (site 30) and brooding of chicks (all other sites) by the male and female parents during two 24-h watches at plot U in 1977

79 Figure 30. Time elapsing between arrival and exchange of brooding duty in relation to age of chicks during three watches at plot S1 in 1977

79 Figure 31. Mean duration of time spent by both members of a pair at the site during exchanges of chick brooding duty in relation to date at plot S1 in 1976 and 1977

81 Figure 32. Rates of arrival of prospecting birds during 24-h watches in 1975 and 4-h watches in 1977 at plot S1

82 Figure 33. Numbers of birds counted on ledges not used for breeding as percentage of total count at plot G1 in relation to date, and changes in the total count of birds, expressed as 7-day means for 1975

82 Figure 34. Proportion of birds observed leaving the cliffs and returning to land more than 20 m from their original point of departure, in relation to date

83 Figure 35. Duration of time spent on plot S1 by individual prospectors, on 23–29 July and 8 August 1977

84 Figure 36. Sketch of plot S1 showing the places where prospecting birds landed during watches in July 1977

85 Figure 37. Sketch of plot S1 showing the routes walked by four prospecting birds watched in July 1977

85 Figure 38. Rates of arrival of prospecting birds in relation to time of day for six watches during incubation and five watches during chick rearing at plot S1 in 1975

86 Figure 39. The proportion of variation in counts made every 2 h at plot S1 explained by the correlation between numbers and the rate of arrival of prospectors and site-holders for 1975

87 Figure 40. Relationship between the frequency of incubation changes and the number of prospectors arriving during 4-h watches at plot S1 in 1977

88 Figure 41. Relationship between the total number of birds present and the number of prospectors arriving during 4-h watches at plot S1 in 1977

89 Figure 42. Contribution of different categories of birds to total numbers present on plot S1 during a 24-h watch on 31 July 1976

90 Figure 43. Contribution of different categories of birds to total numbers present on plot S1 during a 24-h watch on 21 August 1976

91 Figure 44. Frequency of fights on plot S1 in 1975 and 1977 and on plot U in 1977 in relation to date

92 Figure 45. Fights observed at plot S1 in 1977 in relation to the status of birds involved

94 Figure 46. The relationship between the rate of arrival of prospectors at plot S1 and the rate at plot U

95 Figure 47. The relationship between the frequency of fighting at plot S1 and plot U

96 Figure 48. Mean numbers of fights per hour observed at plot S1 for six watches during incubation and five watches during chick rearing in 1975

96 Figure 49. Frequency of fights at plot S1 in relation to the number of prospectors arriving

99 Figure 50. Numbers of chicks observed fledging per 10-min period from cliffs visible from the base of the south spit during the night of 15–16 August 1975

101 Figure 51. Sketch of plot S1 showing the routes taken by some chicks which did not fledge directly from their sites in 1977

118 Figure 52. Cumulative plot of the numbers of new eggs seen per 10-min period by three observers watching plot S1 from 1530 h, 14 July 1977

119 Figure 53. Cumulative plots of the number of new eggs seen per 10-min period by the same observer watching in overcast conditions from 1200 h, 11 July 1977 and in sunny conditions from 0930 h, 12 July 1977, plot S1

120 Figure 54. Distribution of the number of days on which eggs were definitely observed during the incubation period at plot S1, compared with the Poisson distribution for the same mean

124 Figure 55. Distribution of laying dates observed within 48 h at all plots for 1976 and 1977 and at S1 for 1975 and 1977

125 Figure 56. Proportion of eggs replaced in relation to the date on which the first egg was lost in 1977

126 Figure 57. Length of time elapsing between the loss of an egg and the laying of a replacement, for periods known within 48 h in 1977

127 Figure 58. Lengths of incubation periods determined from laying and hatching dates known to within 48 h

128 Figure 59. Cumulative progress of hatching in three seasons expressed in 2-day periods

129 Figure 60. Number of chicks hatching per 2-day period on seven study plots in 1977

132 Figure 61. Numbers of chicks fledging each day in 1975, 1976, and 1977

133 Figure 62. Age at fledging of chicks at all plots in 1976 and 1977, calculated from hatching and fledging dates known within 48 h and 24 h, respectively

134 Figure 63. Comparison of the ages of chicks fledging after a period of moderate winds with those fledging after 2 days of high winds

134 Figure 64. Age at fledging in relation to the date of hatching for all 3 years, 1975–77

139 Figure 65. Rates of loss of eggs and chicks (in 1977) in relation to the time elapsing since laying and hatching

140 Figure 66. Hatching success in relation to date of laying in 1976 and 1977

140 Figure 67. Fledging success in relation to the date of hatching in all 3 years, 1975–77

142 Figure 68. Breeding success in relation to date of laying in all 3 years, 1975–77

147 Figure 69. Proportion of eggs which were laid on sites not occupied in 1976 in relation to the date of hatching in 1977

148 Figure 70. Distribution of adult murres on a representative section of the East Cliff colony

150 Figure 71. Representation of breeding-site characters (1) to (6) of Thick-billed Murres, showing categories for each character

161 Figure 72. Sketch showing the distribution of early-hatched chicks on plot S1 in 1976

162 Figure 73. Sketch showing the distribution of early-hatched chicks on plot S1 in 1975, 1976, and 1977, and all sites where the date of hatching was recorded in all 3 years

172 Figure 74. Volume indices of eggs in relation to ground colour classes

176 Figure 75. Mean length of primary coverts in relation to age for chicks measured at plot S in 1977

178 Figure 76. Growth curves for five chicks selected at random from those weighed on sites at plot S in 1976

178 Figure 77. Growth curves for five chicks selected at random from those weighed on sites at plot S in 1977

179 Figure 78. Mean weights of chicks measured in 1976 in relation to age and smoothed growth curve for the same sample using linear interpolation to estimate weights on days when measurements were not taken

179 Figure 79. Smoothed growth curves for all chicks weighed on plots SA, SB, and SC combined in 1975, 1976, and 1977

180 Figure 80. Mean daily weight increments of chicks weighed on plots SA, SB, and SC combined in 1975, 1976, and 1977 and standard deviations of the increments

182 Figure 81. Smoothed growth curves for two cohorts of chicks weighed on sites at plot S in 1975

182 Figure 82. Smoothed growth curves for early and late chicks weighed on sites at plot S in 1977

183 Figure 83. Smoothed growth curves for two cohorts of chicks weighed on sites at plot S in 1976

183 Figure 84. Growth curves for chicks weighed in 1977 on sites at plots E and S, and coefficients of variation

188 Figure 85. The interaction of parental quality and environmental conditions in determining the growth rates and age at fledging of Thick-billed Murre chicks

192 Figure 86. Mean feeding rates to chicks observed during watches at plot S1 in 1975 and 1976, and at plots S1 and U combined in 1977

193 Figure 87. Feeding rates to chicks observed during 4-h watches at plots S1 and U in 1977 and percentage of chicks measured on sites at plot S which showed more than the median weight increase for their age class

195 Figure 88. Distribution of numbers of meals delivered to chick during the first three 12-h watches after they had hatched in 1975, and the first five 4-h watches in 1977

196 Figure 89. Sketch of study plot S1 showing the position of chicks fed at above the median rate during the first three 12-h watches after they had hatched in 1975 and the first five 4-h watches in 1977

197 Figure 90. Feeding rates of chicks at plot S1 in 1975 and 1976, and at plots S1 and U in 1977 in relation to ages of chicks

198 Figure 91. Feeding rates observed during watches at plot S1 in 1975 for three cohorts

198 Figure 92. Feeding rates of chicks observed at plot S1 in 1975 in relation to the age of the chicks with four watches plotted separately

199 Figure 93. Feeding rates of chicks observed during six watches at plot S1 in 1976 in relation to the date of hatching of the chicks

200 Figure 94. Distributions of time intervals between meals to individual chicks observed during 24-h watches at plot S1 on 31 July and 21 August 1976, and at plot U on 24–25 August 1977

203 Figure 95. Comparison of the sizes of fish picked up from ledges in 1977 with those obtained from chicks fitted with collars

204 Figure 96. Sizes of fish collected from chicks fitted with collars in 1977, in relation to date of collection

213 Figure 97. Mean length of largest testis of Thick-billed Murres at Prince Leopold Island in relation to date

214 Figure 98. Mean diameter of largest oöcyte of Thick-billed Murres at Prince Leopold Island in relation to date

214 Figure 99. Proportion of Thick-billed Murres collected at Prince Leopold Island which had brood patches partially or fully developed or regressing, in relation to date

215 Figure 100. Mean weights of male and female Thick-billed Murres collected or captured at Prince Leopold Island during 1975–77, in relation to three stages of the breeding cycle

219 Figure 101. Numbers of individual crustacea recorded in relation to the number of taxa identified in the stomachs of Thick-billed Murres at Prince Leopold Island

220 Figure 102. Size distributions of *Boreogadus saida* estimated from the lengths of otoliths from the stomachs of Thick-billed Murres at Prince Leopold Island in 1976 and 1977

221 Figure 103. Mean lengths of *Boreogadus saida* taken from Thick-billed Murres at Prince Leopold Island in 1976 and 1977, in relation to the dates on which birds were collected

222 Figure 104. Comparison of size distributions of 19 *Boreogadus saida* specimens from Thick-billed Murres collected at Prince Leopold Island prior to 5 July in 1976 with 688 specimens from birds collected near the edge of land-fast ice during the same period

222 Figure 105. Size distributions of *Parathemisto* spp. obtained from Thick-billed Murres collected at Prince Leopold Island between 30 June and 10 August 1977 and on their feeding grounds in Lancaster Sound in July and August 1976

225 Figure 106. Size distribution of prey taken by adult Thick-billed Murres in Lancaster Sound

226 Figure 107. Comparison of size distributions for arctic cod from adult stomachs during chick rearing and from collared chicks in 1977

229 Figure 108. Numbers of Thick-billed Murres recorded at the edge of fast ice across the southern end of Wellington Channel, in relation to attendance at the Prince Leopold Island colony in 1976

229 Figure 109. Distribution of Thick-billed Murres in the Barrow Strait survey area on 2 August 1976

230 Figure 110. Distribution of Thick-billed Murres in the Barrow Strait survey area on 6 August 1976

231 Figure 111. Distribution of Thick-billed Murres in relation to distance from Prince Leopold Island, 2 and 6 August 1976

232 Figure 112. Distribution of sightings of Thick-billed Murres from CSS Hudson during 17–19 August 1976

233 Figure 113. Distribution of Thick-billed Murres in Barrow Strait survey area on 25 June 1977

234 Figure 114. Distribution of Thick-billed Murres in Barrow Strait survey area on 18 July 1977

235 Figure 115. Distribution of Thick-billed Murres in Barrow Strait survey area on 20 August 1977

236 Figure 116. Rank importance of various ice-edge sectors to Thick-billed Murres, 1974–76

240 Figure 117. Final positions of outbound flocks of Thick-billed Murres watched until lost from view on 5 July 1977, or for 2 min beyond the tip of the south spit on 28 July 1977

241 Figure 118. Mean headings of outbound flocks of Thick-billed Murres watched for at least 2 min beyond the tip of the south spit, in relation to wind speed at the time

244 Figure 119. Alternative routes taken by flocks of Thick-billed Murres passing outbound down the east side of the south spit

248 Figure 120. The genus *Uria* as a proportion of total numbers o seabirds, at different latitudes in the north-west Atlantic and north-east Pacific

252 Figure 121. The position of *Boreogadus saida* in the Lancaster Sound ecosystem

257 Figure 122. Distribution of murre colonies in the western Atlantic and eastern Canadian Arctic, in relation to the occurrence of > 10% ice cover during late July and the first half of August

262 Figure 123. Hypothetical relationship of the ratio of prey densities at a given distance from the colony to densities adjacent to the colony that would make it profitable for Thick-billed Murres to travel that far to feed

262 Figure 124. Hypothetical relationship between colony size and proportion of time available for feeding, assuming uniform prey density

264 Figure 125. Relationships between colony size and mean prey density in surrounding waters, and between colony size and maximum foraging radius

264 Figure 126. Interaction of food depletion and information centre effects in relation to colony size in an unpredictable environment

268 Figure 127. The interrelationship of factors leading towards precocial fledging behaviour in the genus *Uria*

## List of appendices

286 Appendix 1. Study plot photos showing plot boundaries and positions of breeding pairs of Thick-billed Murres within each of the major study plots monitored from 1975 to 1977

299 Appendix 2. Some climatic data collected during the summer months (May–September) at Prince Leopold Island, 1975–77

306 Appendix 3. Daily counts of individual Thick-billed Murres on 12 study plots along the East Cliff colony between 1700 and 1900 h, 1975–77

312 Appendix 4. Instructions for making behaviour watches on study plots G3 and S1

313 Appendix 5. Spearman rank correlation coefficients comparing fluctuations in numbers on all sites counted every 2 h on 11 June 1976 and distances between plots

313 Appendix 6. Spearman rank correlation coefficients comparing fluctuations in numbers of birds counted on all sites every 2 h on 11 July 1976

314 Appendix 7. Details of counts and conversion factors used to calculate an estimate of the size of the breeding population of Thick-billed Murres at Prince Leopold Island in 1975

314 Appendix 8. Details of counts of birds and conversion factors used to calculate an estimate of the size of the breeding population of Thick-billed Murres at Prince Leopold Island for 1976/77

315 Appendix 9. Breeding performance data for pairs of Thick-billed Murres at sites on seven study plots along the East Cliff colony, 1975–77

328 Appendix 10. Dates of laying of first eggs known within 48 h at seven study plots in 1976

329 Appendix 11. Dates of laying of first eggs known within 48 h at seven study plots in 1977

330 Appendix 12. Dates of hatching of first eggs at seven study plots in 1975

331 Appendix 13. Dates of hatching of first eggs at 10 study plots in 1976

332 Appendix 14. Dates of hatching of first eggs at seven study plots in 1977

332 Appendix 15. Dates of fledging of chicks at six study plots in 1975

333 Appendix 16. Dates of fledging of chicks at 10 study plots in 1976

334 Appendix 17. Dates of fledging of chicks at seven study plots in 1977

335 Appendix 18. Duration of chick rearing in relation to date of hatching at study plots G1, G4, S1, and U in 1975

336 Appendix 19. Duration of chick rearing in relation to the date of hatching at all study plots in 1976

337 Appendix 20. Duration of chick rearing in relation to date of hatching at all study plots in 1977

338 Appendix 21. Distribution of sites according to neighbour, wall, and slope characters at seven study plots for 1977 only

339 Appendix 22. Body weight of individual chicks on growth plots in relation to age, 1975–77

344 Appendix 23. Mean number of meals per 4-h period to chicks on study plot S1 in 1977 in relation to age and date of hatching

344 Appendix 24. Measurements of Thick-billed Murres collected at Prince Leopold Island, N.W.T., 1975–77

347 Appendix 25. Details of food organisms identified in the digestive tract of Thick-billed Murres collected at Prince Leopold Island in 1976

347 Appendix 26. Details of food organisms identified in the digestive tract of birds collected at Prince Leopold Island in 1977

348 Appendix 27. Derivation of the formula relating the minimum density ratio to differences in foraging distance between different feeding areas

349 Appendix 28. Derivation of equation [7] relating mean density of prey to colony size

# Foreword

**By Hugh Boyd**

"Science can be defined as all those problems to which this procedure (the method of strong inference) has been successfully applied" (C.H. Waddington, *Tools for Thought*, page 118, Cape, London, 1977). The most exciting feature of the work undertaken by David Nettleship and Tony Gaston, of which this large volume forms a surprisingly small part, is that it is science as well as first rate natural history. They devise hypotheses and ways of testing them so as to obtain clean results, and otherwise behave like scientists, rather than voyeurs. This is the more remarkable because they have been surrounded by the flummery of environmental assessment. David Nettleship has, indeed, contributed notably to the war of words over the future of Lancaster Sound and other splendours of Canada's North. Yet he has contrived to do so without losing sight of his principal objective, adding to our understanding of how part of the marine world really works. As a result he now speaks with the "authority of knowledge", so rightly stressed by Dr. P. McTaggart-Cowan in a recent interview, which must surely in the end prevail over the superficiality that has characterized much ephemerally-funded ecological work in the North.

The work reported here is a superior example of what "baseline studies" should be. It will be comparatively easy for investigators 20, 40 or 100 years from now to make comparisons between the state of some of the biological systems of Lancaster Sound in the 21st century and how they were faring in 1975–77. Such opportunities are far rarer than they should be. The meticulous attention to detail in reporting how tasks were designed and effected, and with what results, makes parts of this book slow going, even for the already knowledgeable. Yet the authors are writing for the investigators of the future at least as much as for their contemporaries.

In the 1950s, Leslie Tuck brought to his pioneering investigation of northern seabird colonies that distinctive mixture of curiosity and irrepressible enthusiasm that carried him over or through all the physical, financial and bureaucratic barriers that surround research in remote places. For most of the time he was a one-man band. Twenty years later ecological research is now a team game. Tony Gaston and David Nettleship acknowledge the fine work accomplished by the members of the teams they led, often in difficult conditions. Yet it is their own determination and skill that have achieved this publication, despite the new crop of investigations that might have constrained those less dedicated to be silent.

"This is all, and indeed rather more than all, that is known to man of the blessed St. Neot; but not more than is known to the angels in heaven" (attributed to J. A. Froude by Lytton Strachey, in Eminent Victorians 1935, page 33). Fortunately *Uria lomvia*, unlike the early saints, is with us yet; and from now on, equipped with a guide to conduct of which Mrs. Beeton, or Emily Post, could well be proud.

# Preface

The Thick-billed Murre *Uria lomvia* is a highly specialized seabird once regarded as one of the most numerous seabirds in the world (Tuck 1961). Specialized organisms, however, requiring a narrow and often fixed environmental regime, are highly vulnerable to decimation because their evolution has proceeded so far that they are incapable of adapting themselves to rapidly changing conditions. The Thick-billed Murre is such a species.

The substantial decreases (20–40%) that appear to have taken place over a large portion of the Thick-billed Murre's range (see recent reviews by Evans and Waterston 1976, Nettleship 1977*a*, King *et al.* 1979, Salomonsen 1979) give rise to major concern for the species' future welfare. The species has suffered heavy mortality both during and after the breeding season because of factors which have either begun, or intensified during the past 30 years. These factors affect the birds directly (e.g., shooting, drowning in fish nets, oil fouling, and disturbance) and indirectly (e.g., toxic chemical poisoning, commercial fisheries developments, and other activities which may reduce the food supply). The future of populations in the western North Atlantic is especially precarious now that extensive areas of the Canadian Arctic and West Greenland are being subjected to the new hazards of deep-water oil drilling and increased shipping of petroleum products, including existing and proposed drilling operations in waters close to major colonies in Lancaster and Jones Sounds, southern Davis Strait, and Hudson Strait. Such massive declines in a species of low effective productivity and imminent threats to critical areas can only be deplored by those interested in maintaining the richness and diversity of marine ecosystems. This presents a major challenge to nations responsible for the welfare of marine bird populations and other living things inhabiting the waters of the Arctic, Atlantic, and Pacific oceans.

The research on Prince Leopold Island was designed and initiated by D.N.N. as part of a major study program undertaken by the CWS on the distribution and ecology of seabirds in eastern Canada. The field study was to cover 5 years, beginning in 1975 and ending in 1979, but it became necessary due to financial constraints to limit the project to 3 years, 1975–77. The Thick-billed Murre study was supervised by D.N.N. with A.J.G. in charge of the field work. Our objective was to gather as much information as possible on the reproductive biology and ecological requirements of Thick-billed Murres breeding at a single location in Lancaster Sound, the gateway to the Northwest Passage. We were concerned principally with aspects of ecology and behaviour which might allow us to predict the effects of environmental changes, particularly those associated with human activities, and we also paid considerable attention to the evaluation of methods in the hope of formulating guidelines for future investigators. The study led us to speculate on the adaptive significance of many aspects of the species' ecology and we hope that these hypotheses will be useful in the generation of new ideas which can be tested in the field.

The original idea of developing a study of seabirds at Prince Leopold Island was conceived in 1972 and the initial objectives (Nettleship 1977*b*) seemed manageable. The task of documenting attendance at the colony, timing of breeding, breeding performance, and feeding ecology, and how these population parameters varied between years remained straightforward and easy to accomplish until put into practice in 1975. It quickly became apparent to us that the problem was more complex. We discovered that within-colony variation in timing, breeding success, chick growth rates, feeding rates, rates of arrival of non-breeding birds, and ratios of breeding pairs to the number of individual birds in attendance was high. This possibility was not recognized at the outset, as we expected the inter-year variation to be the most striking feature of a species reproducing in a relatively unpredictable and changeable environment. Significant within-year variation affected the design of the study and restricted the degree of generalization permissible from an analysis of results based on only a small number of sites (study plots) within a large colony. We hope that the sample sizes used to measure timing, breeding success, and attendance were adequate to account for this intra-colony variation, but sample sizes for chick growth and feeding rates were unavoidably small due to the inaccessibility of chicks (most cliffs used for breeding were unsafe for climbing).

There were other shortcomings as well. The fragile, crumbly cliffs made it impossible to mark large numbers of adults, which precluded studies of survival rates. We only obtained a little information on adult diet as many stomachs examined were empty, probably due to the long distance the birds had travelled to return to the island and the rapid rate of digestion. Finally, economics dictated that we were only able to obtain brief glimpses of the distribution of birds at sea — in fact, on only 10 days through the three seasons (1975–77) of study — to determine patterns in the use of marine habitats.

We have organized this text so that each chapter may be read on its own without the need for extensive cross-referencing. This has resulted in some repetition and a somewhat unorthodox order of appearance of some topics. The intention is to have a more efficient and interrelated set of topics in terms of the understanding of the general life-cycle pattern and reproductive strategies displayed by Thick-billed Murres at Prince Leopold Island. The chapters, therefore, appear in a sequence roughly corresponding to their biological affinities.

In Chapter I, we identify the general features of the study area and our approach to the investigation. Chapter II describes the pattern of attendance at the colony and associated behaviours displayed by the various age cohorts; we also outline the methods used to determine the size of the breeding population. In Chapter III, we analyse the timing of breeding and the levels and determinants of reproductive success both within and between years. Chapter IV describes egg size and colour, and features of chick growth and diet. Chapter V reviews the morphology and diet of adults, and outlines foraging and food-finding characteristics of the population. In Chapter VI, we integrate and synthesize the information given in the preceding chapters and review more generally our views of the biological properties of Thick-billed Murres in Lancaster Sound and the selective forces that shape and limit their specialization and prospects for the future.

The appendices include details of critical parts of the study (e.g., study plot photos) and much of the raw data (daily counts, breeding performance, climatic conditions, etc.) gathered over the 3 years of study. These are intended to provide: (1) a comprehensive baseline for accurately monitoring population levels (size, status, and productivity) of murres over both the short and long terms in a way that enables biologists and wildlife managers to identify species' problems and responsible factors (natural and man-induced), and (2) an opportunity for making direct comparisons with populations examined elsewhere, as well as using the data to re-examine, test or develop new ideas.

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## Résumé

L'étude sur la Marmette de Brünnich de l'île Prince-Léopold a été conçue en 1972, et l'objectif premier de cette étude était d'examiner la fréquentation de la colonie, la période de reproduction, la performance reproductrice, l'écologie de l'alimentation, et les variations interannuelles de ces paramètres. Au cours des travaux sur le terrain, nous avons découvert de fortes variations intracoloniales dans la période et le rendement de la reproduction, le taux de croissance des oisillons, le rythme d'alimentation, le rythme d'arrivée des oiseaux non reproducteurs, et le rapport entre le nombre de couples reproducteurs et le reste de la colonie. Des variations intra-annuelles importantes ont modifié le caractère de l'étude et limité le degré de généralisation permis par une analyse des résultats fondés uniquement sur quelques secteurs d'étude d'une vaste colonie.

Nous avons connu d'autres difficultés. La fragilité et la friabilité des falaises ont empêché le marquage d'un grand nombre d'adultes et, par conséquent, l'étude du taux de survie du groupe. Nous avons peu de données sur le régime alimentaire des adultes car la plupart des oiseaux examinés avaient l'estomac vide, probablement à cause des longues distances parcourues pour revenir dans l'île et d'une digestion rapide. Enfin, pour des raisons financières, nous n'avons effectué que de brefs relevés de la distribution des oiseaux en mer en vue d'étudier l'utilisation de l'habitat.

Les chapitres apparaissent dans un ordre à peu près correspondant au cycle biologique de l'espèce étudiée. Au chapitre I, nous faisons une description générale de la région étudiée et de la démarche adoptée. Le chapitre II porte sur la fréquentation de la colonie et les comportements des divers groupes d'âge; les méthodes de recensement des oiseaux reproducteurs sont également exposées. Le chapitre III est une analyse de la période de reproduction et du degré et des facteurs du rendement reproductif sur une base intra- et interannuelle. Le chapitre IV décrit la grosseur et la couleur des oeufs, ainsi que la croissance et le régime alimentaire des oisillons. Le chapitre V porte sur la morphologie et le régime alimentaire de l'adulte et sur le ravitaillement de la colonie. Au chapitre VI, nous faisons l'intégration et la synthèse des données des chapitres précédents afin de donner une vue d'ensemble des relations entre les Marmettes de Brünnich et leur environnement.

Les annexes fournissent des détails sur des aspects importants de l'étude (p. ex., des photographies des secteurs d'étude) et sur la majeure partie des données brutes (recensements quotidiens, performance reproductrice, conditions climatiques, etc.) rassemblées pendant les trois années de l'étude.

## Acknowledgements

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# Chapter I Introduction

# 1. Background information

In 1971 the Canadian Wildlife Service (CWS) launched a comprehensive multi-species study of seabirds in the eastern Canadian Arctic including Prince Leopold Island (Nettleship 1977*a*, *b*). The overall objective was to obtain data on which to base estimates of population density flux, biomass changes, and bioenergetic demands of seabird populations, especially with reference to the breeding season. These estimates are essential to knowledge of the ecological requirements of seabirds for successful reproduction and for a better understanding of the structure and function of marine ecosystems in northern regions. Moreover, this information is required immediately to answer questions concerning the effects of industrial expansion (especially deepwater oil drilling and transport) in the Arctic on seabird populations and their vertebrate and invertebrate foods.

The study emphasized Thick-billed Murre *Uria lomvia* and Northern Fulmar *Fulmarus glacialis*. The pattern of distribution and abundance of both species makes them valuable indicators of the health of seabird populations in general and of changes in both critical components of existing food webs and interrelationships of the principal species in the eastern Canadian Arctic.

This monograph describes one aspect of that overall study: the work on Thick-billed Murres on Prince Leopold Island in 1975–77. We concentrate on all aspects of the species' breeding biology to ensure an adequate understanding of its environmental needs both within and between study years. We also provide information for improving census techniques used to monitor future changes in bird numbers, for interpreting past census data, and for formulating conservation measures.

Fundamental consideration in the design of the study was the likelihood of major oil and gas developments taking place in the Lancaster Sound region and the high vulnerability of murres to contamination and death by oil at sea. Therefore, we also had to identify precise feeding areas away from the colony and thoroughly understand the pelagic distribution of murres in the Barrow Strait – Lancaster Sound area.

A general account of the biology of the Thick-billed Murre has been given by Tuck (1961). He estimated a total world population for the species at that time of around 20 million birds, 10 million of which occurred in the western Atlantic with numbers divided equally between the eastern Canadian Arctic and the coast of West Greenland during the breeding season. Recent surveys suggest that the species has severely declined in numbers over the last 20 years in both West Greenland (Joensen and Preuss 1972, Evans and Waterston 1976, Salomonsen 1979) and the eastern Canadian Arctic (Brown *et al.* 1975, Nettleship 1977*a*, Gaston and Nettleship 1980). Table 1 gives revised population estimates and these new figures indicate a total breeding population of about 2.3 million pairs of which 56% breed in Canada and the remainder in West Greenland. The importance to the species of very large colonies is underlined by the fact that the seven colonies of 100 000 or more pairs of breeding birds contribute 83% of the total

**Table 1**
Thick-billed Murre colonies and populations in the western Atlantic*

| Colony | Number breeding pairs | Region | Regional total (breeding pairs) |
|---|---|---|---|
| **Eastern Canadian Arctic** | | | |
| Coburg Island | 160 000 | Lancaster Sound | 406 000 |
| Prince Leopold Island | 86 000 | | |
| Cape Hay, Bylot Island | 140 000 | | |
| Cape Graham Moore, Bylot Island | 20 000 | | |
| Reid Bay, Baffin Island | 200 000 | East Baffin | 200 000 |
| Hantzsch Island | 50 000 | Hudson Strait | 665 000 |
| Coats Island | 15 000 | | |
| Digges Sound, 2 colonies | 300 000 | | |
| Akpatok Island, 2 colonies | 300 000 | | |
| **West Greenland** | | | |
| Carey Island | 10 000 | West Greenland | 1 036 000 |
| Saunders' Island | 100 000 | | |
| Agpat | 50 000 | | |
| Agparssuit | 727 500 | | |
| Qaersorssuaq | 13 500 | | |
| Sagdleq Island | 75 000 | | |
| Arveprinsens Island | 25 000 | | |
| Smaller colonies | 35 000 | | |
| **Atlantic Canada** | 2 500 | Atlantic Canada | 2 500 |
| Total breeding population (breeding pairs) | 2 309 500 | | |

*The figures given apply only to the breeding population and do not include pre-breeders or other cohorts of the non-breeding population. Only colonies of more than 10 000 pairs are identified by name. For details of derivation of estimates see Gaston (1980).

breeding population of Thick-billed Murres in the western Atlantic. We therefore urgently need to know much more about the basic ecological requirements of this highly specialized marine species in order to understand the biological significance of changes in murre numbers throughout their range over both the short and long term and to implement necessary conservation measures. This present work attempts to provide some of this fundamental information from which management plans to safeguard the future welfare of migratory bird populations inhabiting northern waters can be constructed.

# 2. Study area

## 2.1. Location and description

Prince Leopold Island (74°02′N, 90°00′W) is located in western Lancaster Sound approximately 13 km from Cape Clarence, the north-eastern corner of Somerset Island, Northwest Territories (Fig. 1). The island is flat topped, oblong, and measures about 11 × 8 km. It forms part of a raised peneplain, with an average elevation of 300 m above sea level.

Lancaster Sound and Barrow Strait form a deep, steep-sided trough, sloping gradually from a depth of 700 m off the Borden Peninsula, north-east Baffin Island, to 140 m off the south coast of Cornwallis Island. The channel separating Prince Leopold Island from Cape Clarence, however, is relatively shallow (about 100 m) and of recent origin (Collin 1962). The north coast of Somerset Island is relatively low-lying, with shallow estuaries at Garnier Bay and Cunningham Inlet. In contrast, the south coast of Devon Island is bounded by cliffs up to 300 m high along most of its length and is cut by a number of deep fiords, of which Radstock and Maxwell bays are the most important. Alluvial areas occur only at the heads of the fiords. The coast of the Brodeur Peninsula is intermediate in character, the cliffs being lower and less steep than those of the south coast of Devon Island but without any major alluvial areas.

Prince Leopold Island is bounded on all sides by vertical cliffs from 245 to 265 m high. On the east and north-east sides of the island these cliffs fall sheer to the sea, but they are covered by basal screes over a half or two-thirds of their height on the south and north sides (Fig. 2*a*). The cliff at the west end of the island is broken into two tiers, separated by a steeply sloping bench, with the lower tier falling sheer to the water. At the north-east and south-east corners of the island gravel spits extend out from the base of the cliffs for about 1 km, sloping gently up to the foot of the basal screes. Access to the beach from the top of the island is possible at only a few spots where the plateau is broken by stream-cut gullies (Fig. 2*b*).

## 2.2. History

Lancaster Sound was discovered and named by William Baffin on 12 July 1616 during his incredible voyage to northern latitudes (Barrow 1818, Taylor 1955). Details of the sound were vague, however, and its existence remained uncertain until rediscovered by John Ross in 1818. Both Baffin and Ross had been impressed by the biological richness of the region.

But it remained for William Edward Parry to penetrate deep into the sound on 1 August 1819, and to note the unusual high abundance and variety of marine birds and mammals found in the region (Parry 1821, 1826; Fisher 1821). On 4 August he sighted and named Prince Leopold Island "in honour of His Royal Highness Prince Leopold Saxe Coburg" (Parry 1821). Heavy ice prevented Parry from closely approaching the island and, as a result, the existence of a major seabird colony there went undetected.

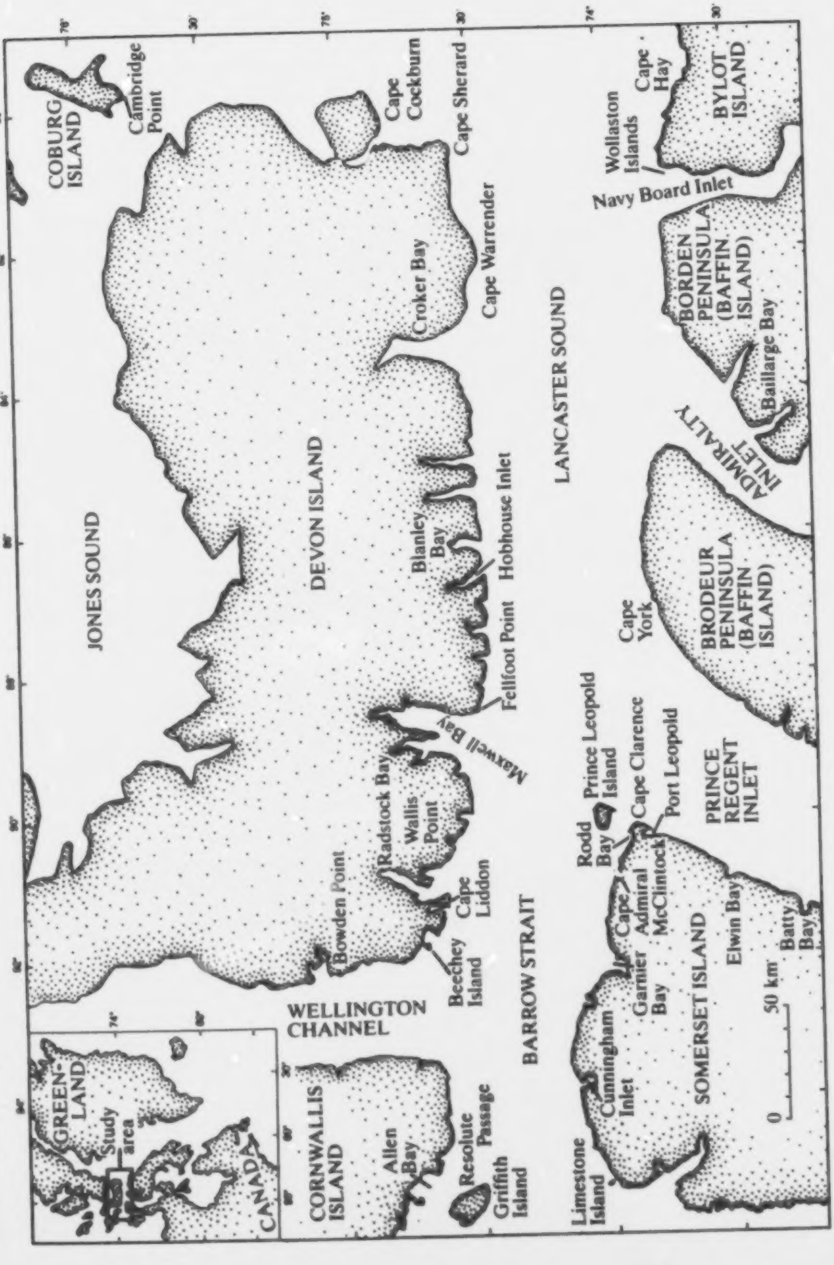
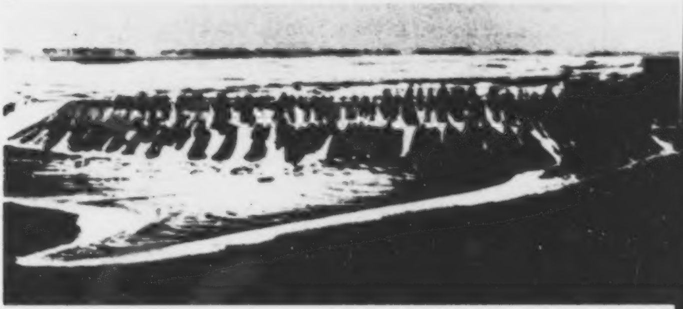

COBURG ISLAND
Cambridge Point
JONES SOUND
DEVON ISLAND
Cape Cockburn
Cape Sherard
Croker Bay
Cape Warrender
LANCASTER SOUND
Blanley Bay
Hobhouse Inlet
Fellfoot Point
Maxwell Bay
Radstock Bay
Wallis Point
Bowden Point
Cape Liddon
Beechey Island
WELLINGTON CHANNEL
BARROW STRAIT
CORNWALLIS ISLAND
Allen Bay
Resolute Passage
Griffith Island
GREEN-LAND
Study area
CANADA
Limestone Island
Cunningham Inlet
Garnier Bay
Cape Admiral McClintock
Rodd Bay
Prince Leopold Island
Cape Clarence
Port Leopold
SOMERSET ISLAND
Elwin Bay
Batty Bay
0
50 km
PRINCE REGENT INLET
Cape York
BRODEUR PENINSULA (BAFFIN ISLAND)
ADMIRALTY INLET
Baillarge Bay
BORDEN PENINSULA (BAFFIN ISLAND)
Navy Board Inlet
Wollaston Islands
Cape Hay
BYLOT ISLAND

**Figure 1**
Lancaster Sound and vicinity

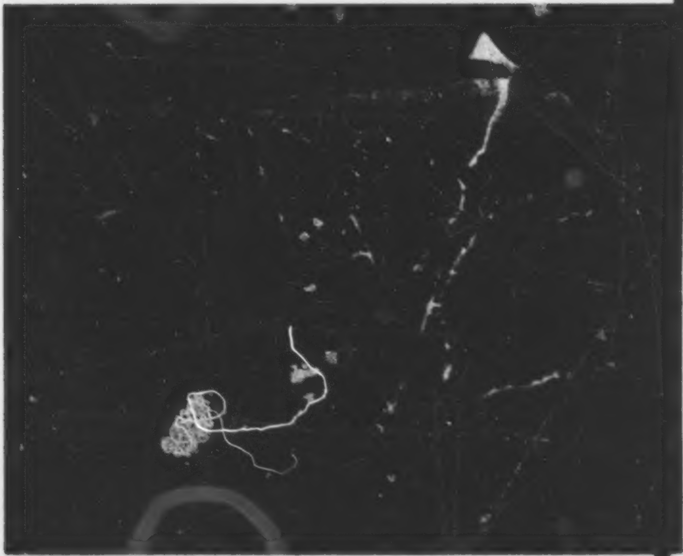
The colony remained essentially unknown to the scientific community for the next 139 years. Obviously, Inuk hunters were well aware of the island's bountiful wildlife resources as evidenced by the numerous whale bones, other skeletal remains, and remnants of prehistoric Inuk dwellings found there. But not until August 1958, when T.W. Barry of the CWS spent 10 days on the island, were the first records made of its breeding seabird colonies (Barry 1961). Surveys in 1972 and 1973 (Nettleship 1974, 1977*b*, Nettleship and Smith 1975, Brown *et al.* 1975) confirmed (within orders of magnitude) Barry's original population estimates.

**Figure 2**
Prince Leopold Island, Northwest Territories: (*a*) oblique view of south spit and south coast, and portion of east cliffs (photo: S.D. MacDonald) and (*b*) vertical view of entire island

*a*



*b*



### 2.3. Seabird populations

Lancaster Sound is most critical to the reproduction and survival of a large proportion of the total seabird community in the Canadian High Arctic. Several million seabirds reproduce and spend the summer in this area, and are dependent upon its biological productivity to meet their energy requirements for growth, reproduction, and maintenance.

The Northern Fulmar, Glaucous Gull *Larus hyperboreus*, Black-legged Kittiwake *Rissa tridactyla*, Thick-billed Murre, and Black Guillemot *Cepphus grylle* are the principal species.

These species are colonial and concentrate during the breeding season where oceanographic conditions supporting a suitable food supply, and cliffs providing suitable breeding sites, occur together. Sites with both properties are rare in the Canadian Arctic and Prince Leopold Island and the surrounding waters is one of them (see also sections 3.2 and 3.4 in this chapter).

Detailed measurements of population levels of the five regular breeders at Prince Leopold Island were made from 1975 to 1977 (Nettleship 1977*a*); these estimates (Table 2) form the first baseline of the numbers of birds present on the island.

The Thick-billed Murre colony comprises, in effect, two colonies. A main one extends about 1 km along the east cliffs from the base of the south spit and a smaller one is situated at the northeast corner of the island (Fig. 3). Northern Fulmars nest on all sides of the island, except for a section of the north cliffs (Fig. 3), whereas Black-legged Kittiwakes nest intermingled with murres on both the East Cliff and North Spit colonies, although they are more numerous at the north spit. Black Guillemots are concentrated at the west end of the island where they nest among the talus and rock crevices on the cliffs. The relatively small population of Glaucous Gulls is dispersed along the west, south, and east sides of the island and also forms small

**Table 2**
Populations and general breeding distributions of seabirds at Prince Leopold Island, 1975–77*

| Species | Number breeding pairs | Census date | Distribution |
|---|---|---|---|
| Northern Fulmar | 62 000† | 1977 | Almost continuously around the cliffs |
| Glaucous Gull | 200‡ | 1975 | Scattered continuously around the cliffs |
| Black-legged Kittiwake | 29 000‡ | 1975 | Two colonies, SE and NE cliffs, intermingled with murres |
| Thick-billed Murre | 86 000† | 1976–77 | Two colonies, SE and NE cliffs |
| Black Guillemot | 4 000§ | 1977 | Two major concentrations along W and NW cliffs, small numbers scattered elsewhere |

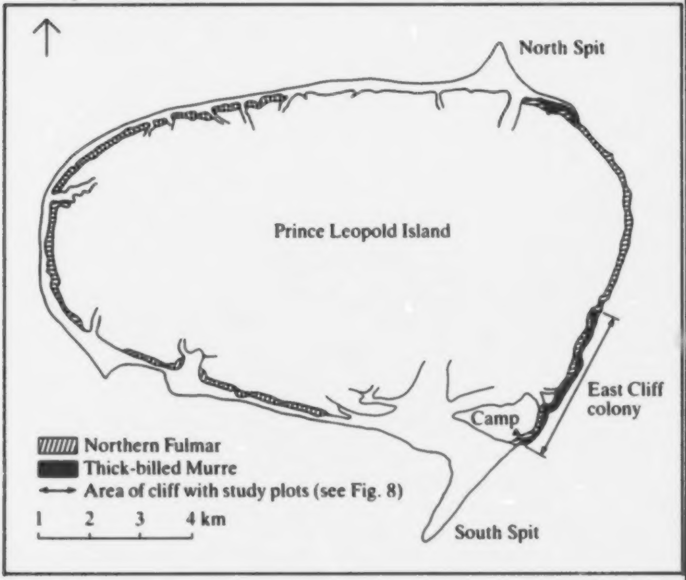
* The figures given for each species apply only to the breeding population and do not include pre-breeders or other cohorts of the non-breeding population. All census details (Nettleship 1976) are filed in the CWS Seabird Research Unit, Bedford Institute of Oceanography, Dartmouth, Nova Scotia.

† Based on detailed examination of population.

‡ Provisional and requires further analysis.

§ Rough estimate.

**Figure 3**
Sketch map of Prince Leopold Island showing physiographic features, location of research camp, and East Cliff colony study area, and the general breeding distribution of Northern Fulmars and Thick-billed Murres. (See Figure 2*b* for further detail of the top of the island)



colonies (10–25 pairs) at the base of the south-east spit and on narrow screes below the East Cliff colony.

The only other significant colonies of seabirds within the Lancaster Sound region are of fulmars at Cape Liddon (10 000 pairs), Hobhouse Inlet (25 000 pairs), and Baillarge Bay (30 000 pairs). There are also mixed populations of murres and kittiwakes at Coburg Island (murres, 160 000 pairs; kittiwakes, 30 000 pairs), Cape Hay (murres, 140 000 pairs; kittiwakes, 20 000 pairs), and Cape Graham Moore, south-east Bylot Island (murres, 20 000 pairs; kittiwakes, 3000 pairs). Figures for breeding populations away from Prince Leopold Island and Coburg Island are estimates only (based on incomplete or old censuses).

### 2.4. Flora and other fauna

Five terrestrial bird species breed regularly on Prince Leopold Island: Brant *Branta bernicla*, Common Eider *Somateria mollisima*, Parasitic Jaeger *Stercorarius parasiticus*, Common Raven *Corvus corax*, and Snow Bunting *Plectrophenax nivalis*. Of these terrestrial species, only the Common Raven, with one or two pairs breeding successfully in each year, and the Parasitic Jaeger, which breeds in very small numbers, are of potential significance to the seabird community.

There is a paucity of vegetation on the island and it is totally absent in many places. Small, scattered patches of vascular plants occur on the gravel beaches and spits (mainly *Saxifraga* spp., *Draba* spp., *Papaver radicatum, Dryas integrifolia, Stellaria laeta, Cerastium* sp., etc.), but vegetation is very sparse on top of the island and is virtually restricted to a dense "turf" of lichens (e.g., *Cladonia*) along the east cliffs above the seabird colony. Thick mats of tussock grasses and *Oxyria digyna* also occur on some of the sea cliffs where Northern Fulmars nest in greater numbers.

There are no resident land mammals on the island, although Peary caribou (*Rangifer tarandus pearyi*) and arctic fox (*Alopex lagopus*) probably visit infrequently during winter and ice breakup. Nettleship *et al.* (1980*a*) review all the birds seen on the island during the present study.

The waters immediately adjacent to Prince Leopold Island attract marine mammals throughout the summer, particularly large concentrations (100 + individuals) of beluga (*Delphinapterus leucas*), which were often seen feeding in waters off the east cliffs. Narwhals (*Monodon monoceros*) are also common in smaller numbers, and in 1975, we frequently saw up to 20 walrus (*Odobenus rosmarus* during July. During the periods when the edge of the fast ice in Barrow Strait is connected to the island, we often saw polar bears (*Ursus maritimus*) hunting near the floe edge where ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) are common. Our sightings of marine mammals correspond with those made by Parry (1821, 1826) and Fisher (1821), and together indicate that the waters off the island are rich in marine life throughout the summer and have been for a considerable period of time.

# 3. Physical environment

## 3.1. Summer climate

During the study period the air temperatures varied by only a few degrees during each day from a high at 1500 h to a low at 0200 h. Mean daily temperatures during 3 years ranged between –10 and + 10°C, with an overall mean of about 0°C from late May through to the second half of September (Fig. 4). There was a difference between temperatures at sea level and those at the camp on top of the cliff about 300 m above. Snow often persisted on the top of the island when it had melted at sea level, and there was a considerable difference in the timing of flowering for plant species growing at both levels.

High winds are prevalent in the Lancaster Sound – Barrow Strait region (Taylor 1977), and average winds of 15–20 km/h occurred on most days (Fig. 4). Wind speeds over 50 km/h were not uncommon. On several occasions winds were sufficient to make walking against them on top of the island impossible. In 1975 and 1976 the prevailing wind direction throughout the season was from the west-north-west to north-west, but in 1977, particularly in the latter half of the season, north-east winds were frequent. Strong winds were often accompanied by freezing rain or thick mists causing rime to develop on all exposed surfaces. Precipitation was very low but quite frequent. Snow fell in May and June and from the second half of August, although in 1976 there was a snow storm as late as 13 July.

Fog frequently obscured visibility (Fig. 4). On numerous occasions the top of the island and the surrounding sea were clear, while a thin band of fog hung along the east cliffs. Fog limited observations, particularly in 1975, when visibility of less than 1 km was recorded on 50% of days in June, July, and August.

Barometric pressure fell steadily during May, June, and early July in 1975, rising again during the second half of July and August. In 1976 pressure was also high in May, but fell sharply in early June and fluctuated erratically thereafter. In contrast, in 1977, although pressure was highest in early June, it remained relatively stable throughout the season. Periods of low pressure were associated with high winds and fog on the island, while high pressure generally brought moderate winds and clear skies.

In summary, the summer climate (May–September) at Prince Leopold Island is cool, mainly cloudy with a frequent occurrence of fog, precipitation (rain, freezing rain, snow), and high winds. The 1976 summer was the coolest during the study period; the temperature regimes in 1975 and 1977 were similar. Some climatic data recorded at Prince Leopold Island between 1975 and 1977 are given in Appendix 2; complete records of climate are filed with Polar Continental Shelf Project, Department of Energy, Mines and Resources, Ottawa.

**Figure 4**
Some climatic conditions recorded during the breeding season at Prince Leopold Island, 1975–77, showing (*a*) 7-day running mean of average daily air temperatures and (*b*) 7-day running mean of average wind speeds (daily averages calculated from readings taken at 0700 and 1900 h, CDT). Days on which fog occurred (horizontal visibility < 1.0 km) are denoted along bottom axis by ●

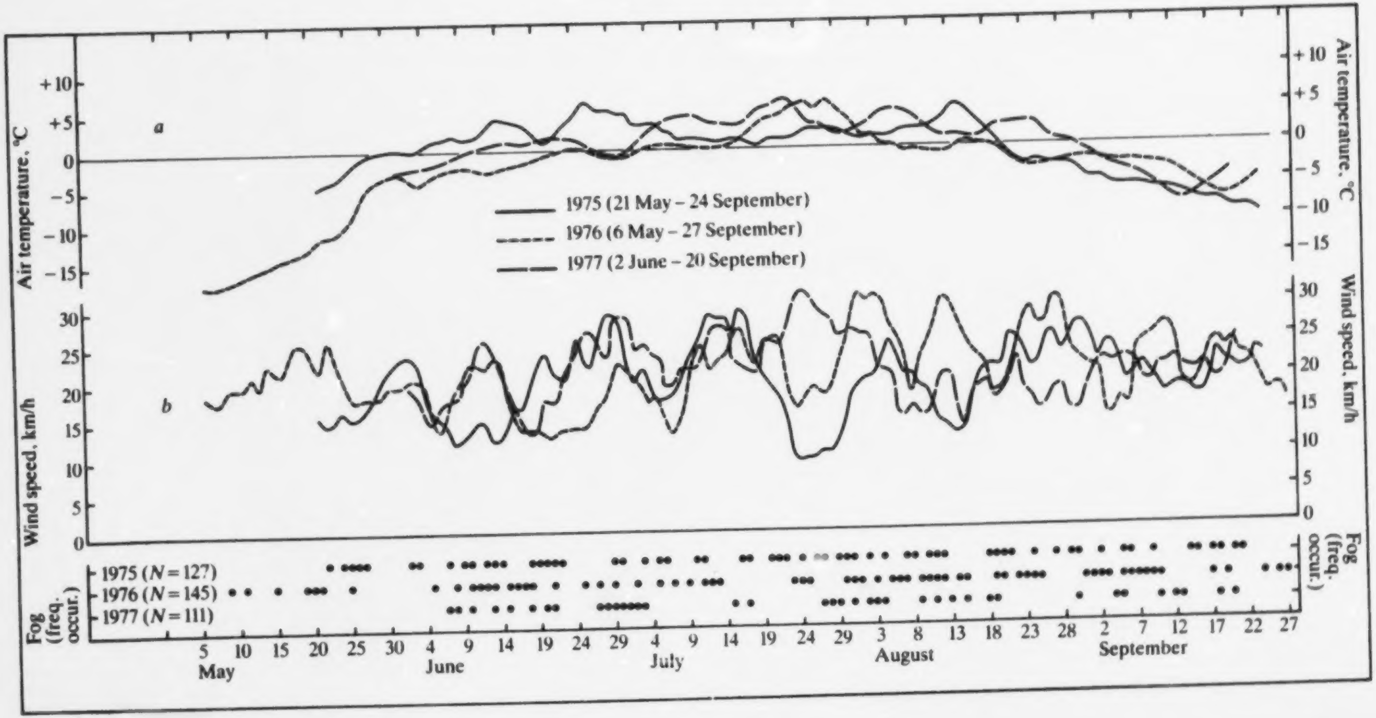
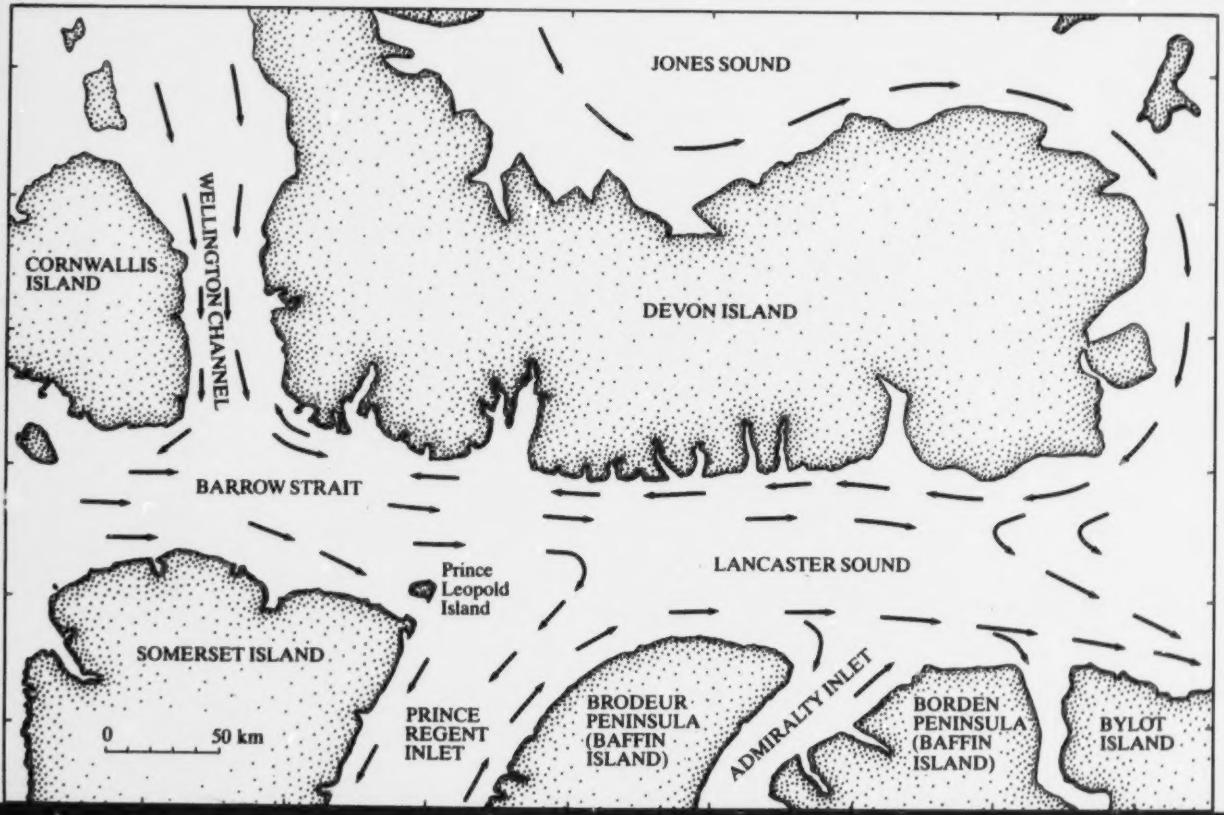


Figure 5
General pattern of surface currents in Barrow Strait – Lancaster Sound (after Bailey 1957, Collin 1962, and Milne and Smiley 1978)


JONES SOUND
CORNWALLIS ISLAND
WELLINGTON CHANNEL
DEVON ISLAND
BARROW STRAIT
LANCASTER SOUND
Prince Leopold Island
SOMERSET ISLAND
PRINCE REGENT INLET
BRODEUR PENINSULA (BAFFIN ISLAND)
ADMIRALTY INLET
BORDEN PENINSULA (BAFFIN ISLAND)
BYLOT ISLAND
0
50 km

### 3.2. Currents

Strong currents flow south through Wellington Channel and east through Barrow Strait from Viscount Melville Sound and into Lancaster Sound, where they converge and meet a distinct current flowing westward along the south coast of Devon Island (Fig. 5). There is also a significant water transfer south from Barrow Strait through Prince Regent Inlet.

This interaction of major currents in the vicinity of Prince Leopold Island and western Lancaster Sound may cause a local enrichment of nutrients that promotes the production of phytoplankton (Dunbar 1951, 1968, 1977) and in turn accounts for the highly diverse and large seabird community at Prince Leopold Island. The oceanographic features of the Lancaster Sound region have been described in detail by Bailey (1957) and Collin (1962), and recently summarized by Milne and Smiley (1978).

The pattern of surface currents in the waters immediately adjacent to Prince Leopold Island are complex, with strong currents of at least 2 km/h flowing north and south along the east side of the island, reversing with the tides. These currents are responsible for the rapid erosion of the east cliffs, which are considerably undercut in places. The gravel spits are the result of the deposition of material eroded from the east cliffs and they are shaped by eddy currents which form in the bays to the west of the spits. Tidal currents also flow in both directions along the south coast, although the general movement of water is eastwards.

### 3.3. Ice conditions

In most years Lancaster Sound – Barrow Strait and associated channels are covered by ice from November to May (Lindsay 1975). An area of open water frequently remains to the east of Prince Leopold Island, however, perhaps maintained by the strong currents. Other smaller polynias also occur to the north-east of Cornwallis Island. The overall timing and pattern of ice breakup in the area is fairly predictable from year to year.

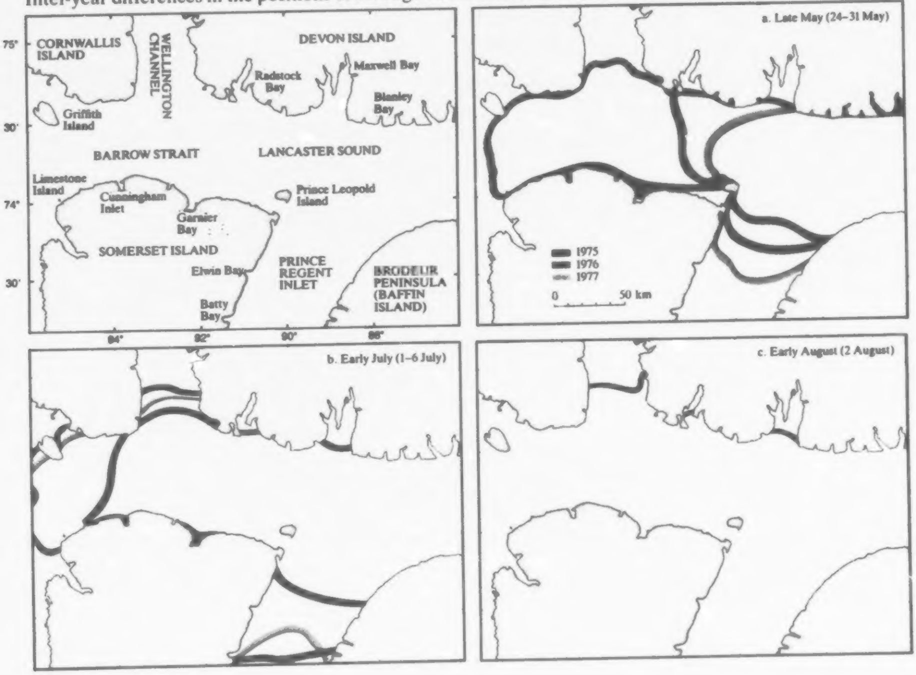
Figure 6 gives the positions of ice edges and timing of ice breakup during the years of study 1975–77 (Alliston *et al.* 1976, Nettleship and Gaston 1978). Bradstreet (1979) summarizes the overall pattern of ice breakup and positions of ice edges in the Barrow Strait for 1974–76 and Marko (1977) and Milne and Smiley (1978) review that information for Lancaster Sound.

### 3.4. Structure of the breeding cliffs

Prince Leopold Island is composed of flat-lying sedimentary rocks of Silurian age. They are calcareous and sediments range from marls to coarse mudstones. Cleavage varies with the type of sediment, being well developed in most cases along bedding planes, so that the rocks tend to fracture into flat slabs 1–10 cm thick. On the top of the island frost-heaving has brought these slabs into a vertical position in places, giving the impression that someone has planted a field of broken dinner plates.

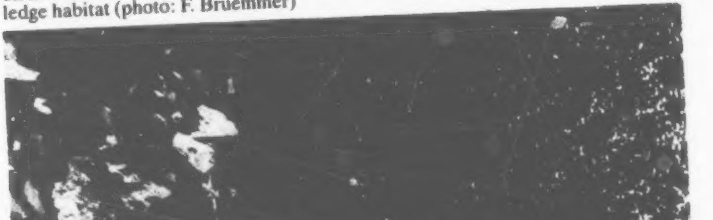
The horizontal cleavage of the rocks results in numerous small ledges on which the murres (Fig. 7) and kittiwakes breed. The east cliffs are eroding very rapidly and immediately after the ground begins

Figure 6
Inter-year differences in the positions of ice edges in the Barrow Strait – Lancaster Sound area, 1975–77


75°
CORNWALLIS ISLAND
WELLINGTON CHANNEL
DEVON ISLAND
Radstock Bay
Maxwell Bay
Blanley Bay
Griffith Island
30'
BARROW STRAIT
LANCASTER SOUND
Limestone Island
Cunningham Inlet
Prince Leopold Island
74°
Garnier Bay
SOMERSET ISLAND
Elwin Bay
PRINCE REGENT INLET
BRODEUR PENINSULA (BAFFIN ISLAND)
30'
Batty Bay
94°
92°
90°
88°
a. Late May (24–31 May)
1975
1976
1977
0
50 km
b. Early July (1–6 July)
c. Early August (2 August)

to thaw in June rocks fall frequently, continuing with diminishing intensity until August. The topography of the cliffs is therefore continually changing. Danger of rock falls made it unwise to visit the base of the east cliffs after mid June and climbing on the cliffs was also difficult. Frost-shatter was so severe in most places that it was impossible to rely on any handhold and impossible to climb without dislodging showers of loose rocks on the birds breeding below. This problem restricted access to breeding ledges to those near the top of the cliffs.

**Figure 7**
Thick-billed Murres on section of East Cliff colony showing density of breeding birds and characteristics of the frost-fractured and horizontal cleavage of the rock-ledge habitat (photo: F. Bruemmer)



# 4. Study techniques

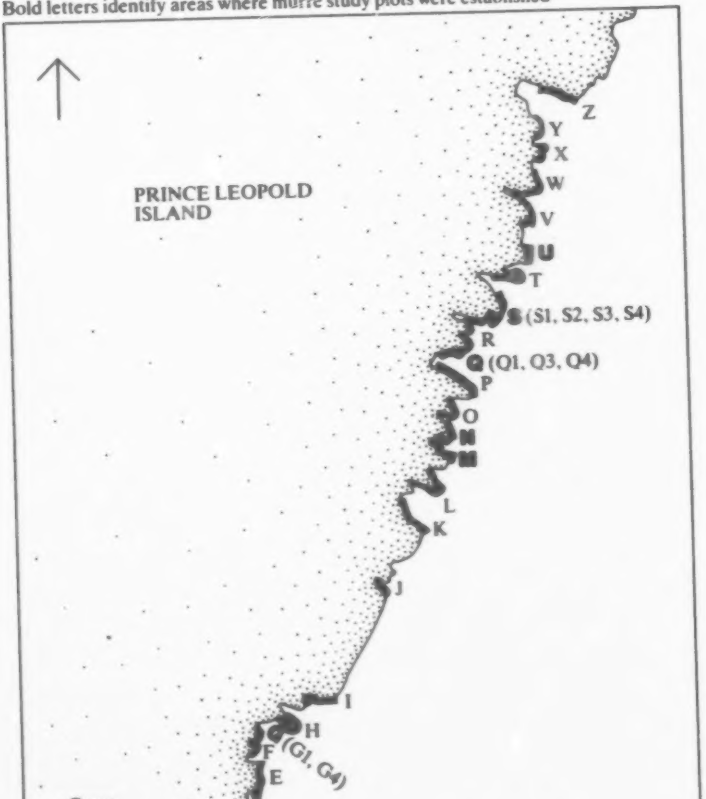
The research camp at Prince Leopold Island was at the top south-east corner of the island and within a few hundred metres of the main murre colony (Fig. 3). The field team worked from 18 May to 24 September 1975, 5 May to 25 September 1976, and 2 June to 22 September 1977. The size of the field team for all the individual species studied varied from five to eight people between years with the largest number in 1976 when fulmars, kittiwakes, and murres were all studied intensively. The number of full-time field workers on the murre project was two in 1975, and three in 1976 and 1977. Thus, early observations in May were limited to 2 of the 3 years of study whereas observations beyond the termination of adult and juvenile emigration (i.e., the fall exodus) were made in all years.

We observed murres breeding on land at specific study plots (see below) and also made observations from boats. In each season we examined (1) population distribution, abundance, and attendance; (2) timing and performance of breeding; and (3) food and foraging habits. The data gathering and analysis of breeding distribution, and the determination of the size of the breeding population were based on methods outlined by Nettleship (1976) and more recently reviewed in Birkhead and Nettleship (1980). We aimed the census program at determining the size of the breeding population and establishing a monitoring system from which future changes in population level could be detected and measured with precision. To assist in the evaluation and comparison of data collected either at other colonies or in future years, we tried to standardize the procedures used, although some adjustments were required as a result of experience obtained during the first season. The work program extended over three seasons to gain some idea of the scale of inter-year variations of the various population variables measured. We observed a number of study plots scattered along the East Cliff colony to assess variation between birds in different parts of the colony.

At the start of the study in May 1975 we used helicopters to survey the cliffs, used by all seabirds for breeding. Using those data, combined with ground and boat surveys made during the pre-laying period, we mapped the general distribution pattern of cliff-nesting birds around the island (Fig. 3) and identified areas suitable for detailed study along the East Cliff colony (Fig. 8). From within these large key headland areas of breeding birds, each of which was assigned a letter (i.e., AA to Z), we selected smaller study plots for each individual species project and used them to obtain data on timing of breeding, number of breeding pairs (density), and breeding success of pairs within each study plot. Where more than one study plot was situated on the same headland, we gave each a separate number to combine with headland letter designation (study plots G1, G4, etc.). We referred to cliff faces by their headland designation and orientation ($S_s$ = S, south facing; $S_n$ = S, north facing, etc.). The overall study approach is outlined in Nettleship (1977*b*) and specific details of techniques employed for each component of the murre investigation are presented in the individual chapters.

Initially, we delineated 15 study plots along the East Cliff colony for studies of murres during the pre-laying period in 1975. Although we intended to include a representative sample of different parts of the colony (i.e., a series of plots which would give as complete coverage as possible of the range of conditions used by the species for breeding), we found that only areas on the upper third of the cliffs were close enough for satisfactory observation. Thus, we selected 12 study plots (Fig. 8) from the original 15 in June 1975 to include a sample of all different types of ledge and different aspects used for breeding, and the number of pairs breeding on each plot was expected to range from 50 to 100. However, study plot S1, where visibility was exceptionally good under all weather conditions because of the short viewing distance, was deliberately made much larger, with about 170

**Figure 8**
Locations of major headlands and general study areas along the East Cliff colony. Bold letters identify areas where murre study plots were established



pairs, to ensure that some observations could be recorded even when bad weather (i.e., poor visibility due to fog and/or blowing snow) precluded examination of most other study plots. We used the 12 study plots to monitor daily attendance at the colony throughout 1976 and 1977, but shortage of workers limited the number in 1975 to nine plots, of which only G1 and G4 were counted regularly. Only 7 (G1, G4, N, Q1, Q4, S1, U) of the 12 plots were used to measure breeding success.

To enable exact replications of counts and observation of breeding performance, all study plots were photographed and delineated on 20 × 25 cm black-and-white photo enlargements and the positions from which the photos and observations were made are marked with permanent rock cairns at the cliff top. The general positions of the study plots referred to in the text are marked in Figure 8 and photos of each study plot showing the precise positions of breeding pairs of murres are given in Appendix 1. Individual breeding sites were marked on the field study plot photographs, numbered, and referred to by their study plot/site number designation (S1/56 = study plot S1, murre pair 56, etc.). In 1975 we numbered sites only when egg laying was observed (as status of birds within each study plot was unknown). In 1976, however, we renumbered those sites so that numbers ran consecutively along ledges. This made recalling the number of a particular site much easier.

The cliffs on which the main murre colony is situated are greatly indented, with numerous minor headlands, in some cases forming isolated stacks (Fig. 8). Thus we could view many areas of cliff straight-on from the opposite headland, which greatly facilitated observations. We erected two plywood blinds overlooking study plots S1 and Q in 1975, and established a third at study plot G in 1976 and another at plot U in 1977. These wood blinds made it possible to continue taking observations when weather conditions would otherwise have made it impossible or ineffective.

We also surveyed the water area around Prince Leopold Island from the air on five dates in 1976 (August and September) and three in 1977 (June, July, and August) to determine the distribution of birds away from their breeding sites and to identify areas which were important to them for feeding during the crucial period when chicks were being reared (Nettleship and Gaston 1978). Information on bird distribution at sea in the Barrow Strait area was also available from similar aerial surveys conducted in the summers of 1974 (Davis *et al.* 1974) and 1975 (Alliston *et al.* 1976), and from surveys carried out at the Allen Bay and Wellington Channel ice edges in 1976 (Bradstreet 1977). Bradstreet (1979) reviews distributions at sea in the Barrow Strait area during the "spring" periods (1 June – 20 July) of 1974–76. Data on the food of adult murres determined from samples collected on their feeding grounds in 1976 were also available from studies made by Bradstreet (1976, 1977) in eastern and western Lancaster Sound.

The statistical procedures for non-parametric tests are exclusively from Siegel (1956) and those for parametric tests from Sokal and Rohlf (1969). We used programs provided by the Statistical Package for the Social Sciences (Nie *et al.* 1975) for multiple linear regression analysis and 2- and 3-way cross-tabulation of breeding success in relation to breeding site characteristics (see Chapter III) and other analyses involving large quantities of data.

# Chapter II Attendance and behaviour at the colony

# 1. Introduction and methods

One of the most pressing problems confronting those concerned with the management of seabird populations is the need to find satisfactory census techniques that will yield consistent results. The size of many colonies presents difficulties and in the case of murres, which do not build nests, the actual definition of a breeding bird may become a matter for subjective interpretation. Our objectives at Prince Leopold Island were (1) to obtain an accurate census figure for the population, (2) to examine methods for monitoring population trends through the establishment of representative study plots, and (3) to study all aspects of behaviour and environmental factors that influence attendance patterns at the colony and hence affect the interpretation of census counts.

Egg-breakage and egg-shell thinning are both associated with high levels of toxic chemicals in the eggs and in the bodies of adult birds. In Common Murres egg-shell thinning has occurred in California, probably as a result of toxic chemical contamination (Gress *et al.* 1971). In some instances high levels of toxic chemicals may have caused aberrant behaviour in breeding birds and this may have contributed to the association between toxic chemicals and egg-breakage (Ratcliffe 1970, Wiemeyer and Porter 1970, Presst and Ratcliffe 1972). For this reason we also wanted to collect baseline data on the behaviour patterns of the Prince Leopold Island murres to provide a basis for comparison if toxic chemicals became implicated in lowered breeding success at some future date.

Thus our observations on behaviour were designed to supplement data on the ecology of the species with the following objectives:

(1) to monitor fluctuations in the number of murres present on the Prince Leopold Island colonies in relation to time of year, time of day, and weather conditions so that census data could be accurately interpreted;
(2) to establish the relative roles of breeding and non-breeding birds in determining changes in the number of birds present;
(3) to record baseline data on the frequency of certain behaviour patterns which could be used for comparative purposes at a later date either at Prince Leopold Island or elsewhere;
(4) to study the incidence of intraspecific aggression within the colony and its relationship to breeding success; and
(5) to study the roles of the sexes during the breeding cycle.

In 1975 most observations were designed to provide information on the average frequency of different behaviour patterns within the population, whereas in 1976 and more particularly in 1977 they were designed to record in detail the behaviour of individual birds of known status. We observed behaviour during the pre-laying period mainly in 1975, and the roles of the sexes only during the second half of the 1977 season.

### 1.1. Colony attendance

Seasonal variations in the number of birds present on the East Cliff colony were monitored by counts made daily between 1700 and 1900 h at plots GI and G4 in 1975, and at plots G1, G4, M, N, Q1, Q3, Q4, S1, S2, S3, S4, and U in 1976 and 1977 (App. 3). Diurnal variation in attendance was measured by counts made every 3 h in 1975 and every 2 h in 1976 through a 24-h period. These counts were made once during the pre-laying period in 1976, and during the incubation and chick-rearing periods in 1975 and 1976. We also took time-lapse cine-films (one frame per minute over 24 h) at plot S1 every 10 days throughout the season in 1976 and 1977. Counts of the number of birds present on the plot were then made on a movie editor, after the field season.

### 1.2. Behaviour

In 1975 we observed plot G3 daily during the pre-laying period, between 3 and 20 June, using a spotting scope. To maintain a constant sample size, the magnification of the telescope was adjusted so that the field of view included about 200 birds each time. The number of birds was counted at the start and end of each watch, and counts were also made at the same time on plots G1 and G4 to monitor the proportion of the daily count population present during each watch (G3 was not included in the daily count because the high density of birds made it difficult to count the entire plot).

Watches lasted from 15 to 75 min and during this period we recorded all arrivals of individual birds, copulations, attempted copulations, and fights. These and similar observations were made at regular intervals (ca. every 3 days) throughout the breeding season in 1976.

In 1975 observations on behaviour during the incubation and chick-rearing periods were made over 24 h every 5 days at plot S1, initially for alternate hours, but after 14 August, continuously. In 1976 watches were carried out only during the chick-rearing period between 0800 and 2000 h every 5 days. The 1977 watches were carried out simultaneously at plots S1 and U every 3 days during the incubation and chick-rearing periods, between 1400 and 1800 h. Three observers rotated watches in 1977 to avoid the possibility of observer bias in inter-plot comparisons. Recording methods were similar in all three years (App. 4).

During the incubation and chick-rearing periods we noted the same parameters as during the pre-laying period, except that we recorded the times of arrivals at occupied sites and of incubation exchanges to the nearest minute. In 1977 two observers watched simultaneously at plot S1 and recorded the times of departures from selected sites; thus, the total time spent on the plot by both members of a pair could be calculated. Arrivals of prospecting birds were tallied on a hand-counter and the totals recorded every hour (the criteria used to distinguish between site-holders and prospectors are given below). We recorded the total number of birds present on the plot every 2 h.

During behaviour watches, we observed only the area of plot S1 indicated in Appendix 1, which included about 160 breeding pairs. In 1977 intermittent watches were carried out during the incubation and chick-rearing periods at S1 to record the behaviour of individual prospectors after they landed on the site. Outline drawings of the plot were used to plot the movements of birds and the position of interactions with other birds. Because birds were not marked, the observer had to watch each bird continuously from landing to departure. During another series of observations made at plots G3, G1, or on the lower cliffs below A, we recorded the fate of birds leaving the cliffs, each bird being followed through binoculars until it either landed on the sea, returned to the cliff, or was lost from view.

To study the role of the sexes in incubation and chick rearing, five birds at plot U were captured on 5 July 1977, and marked with picric acid on the flanks and tips of the secondaries and with coloured plastic PVC (polyvinyl chloride) bands on the right leg to distinguish individuals. The birds were captured while incubating and their eggs were removed. As a result, the pairs began copulating frequently, allowing their sexes to be identified. All subsequently relaid. The sex of another pair could be identified by their plumage. We studied the differences in behaviour between the sexes of these six pairs during regular 4-h watches at U and also during two continuous 24-h watches in late August 1977.

## 2. Descriptions of behaviour patterns

### 2.1. Arrival

Birds arriving at a site already occupied by their mate normally landed within a few centimetres of the sitting bird. The sitter rose instantly, arching its neck and pointing its bill obliquely downwards, at the same time uttering a loud "arrr" call. The arriving bird thrust its head forward beneath the breast of its mate, then both stood up and usually nibbled at one another's bills for a few seconds. Prior to laying, this greeting was often followed by copulation. After laying, incubation exchanges sometimes occurred immediately after the greeting ceremony, with the sitter shuffling backwards off the egg and the arriving bird moving forward simultaneously to cover it. More often, however, the original sitter resumed incubation for some time, during which it was usually preened by its mate. Birds waiting to take over incubation spent a lot of time nibbling around the base of their mate's bill or preening the mate on the head. Occasionally they attempted to "shoulder" the other bird off the egg, but in most cases the exchange was initiated by the incubating bird standing up.

When a chick was present the sequence of events after an arrival was very similar, except that if the arriving bird was carrying a fish it thrust the food under the brooding bird as soon as it stood up and the chick normally seized and swallowed the fish within a few seconds. Both parents remained standing while the chick ingested the fish.

The actions involved in the greeting ceremony allow the arriving bird to see immediately whether its mate is incubating or brooding, or whether there is no egg. This information presumably determines the subsequent behaviour of the pair and the transition from one pattern of behaviour to another can be extremely rapid. In one instance, where an egg had just been lost, the arriving bird (a male) departed immediately after the greeting ceremony, returning a few minutes later and copulating successfully as soon as it landed.

Prospecting birds, not associated with particular sites, stood with wings raised after landing, often continuing to flap for several seconds. After folding their wings they stood with necks stretched and bills obliquely raised, turning the head from side to side. At this stage the carpus was kept clear of the breast feathers. Those birds rarely sat down, but after retracting the neck to assume a normal stance, they often preened their wing coverts, bending the neck sideways to reach them. Standing with wings raised, pointing the bill obliquely upwards, and preening the wing coverts (side) have all been characterized by Birkhead (1978*a*) as submissive behaviour in the Common Murre.

From the start of egg laying to the middle of the fledging period, all sites were almost always occupied. Hence birds arriving at the site usually greeted the sitting bird immediately; we identified these as site-holders. If no such greeting took place, we identified the arriving bird as a prospector.

If during this period an egg had been lost and relaying had not yet occurred, a site was sometimes vacant for several hours. We identified birds that landed at a vacant site and sat down immediately as site-holders and those that remained standing with necks stretched and wings raised as prospectors.

After the chicks had fledged we identified birds that landed on previously occupied sites as site-holders and those that landed on other parts of the plot as prospectors. This identification was somewhat subjective, however.

During the incubation period pairs that did not lay eggs gradually occupied vacant sites. At first, when these pairs visited their sites for only short periods, we recorded them as prospectors, but later on, once they began to greet each other, we recorded them as site-holders. Assuming that the same individuals were involved, it seems a few birds changed categories during the season, slightly affecting the relative rates of arrival recorded for prospectors and site-holders. The proportion of sites established by non-breeders during the 1977 season (when such sites were most numerous) amounted to less than 5% of the total occupied sites and hence the effect was small.

### 2.2. Copulation

Before copulation the pair often preened each other and nibbled at each other's bill. The female then crouched on the breeding site and the male mounted, steadying itself with its wings and sometimes grasping the feathers of the female's crown in its bill. Cloacal contact usually lasted 3–10 s and while the male remained on her back, the female gave a loud, di-syllabic call "cu-cauk" once or twice every second. Following copulation, birds often preened their coverts.

Copulation attempts during which the female did not co-operate, but stood up and pecked at the male, were termed "attempted copulations"; some were probably attempted rapes. Cloacal contact did not occur during these interactions.

### 2.3. Aggression

Aggressive behaviour by Thick-billed Murres was almost entirely directed at members of their own species. A few incidents were observed between murres and kittiwakes, but for the most part there was sufficient segregation between the breeding sites of the two species for little interaction to take place.

Intraspecific aggression ranged in intensity from posture displays to lengthy fights, the participants pecking one another or, at high intensity, grappling with their bills and beating one another with their wings. Pecking was not usually followed by intense fighting and most pecks failed to hit the adversary. Instead, pecking was usually directed towards the head of the other bird and appeared to constitute threat behaviour in situations where the birds did not intend to escalate the intensity of the interaction. Once two birds were committed to fighting, they usually grappled immediately with their bills, locking their mouths and attempting to drag each other off the ledge. These fights frequently ended in both birds falling off the ledge, and they sometimes remained locked together until they hit the sea, where fighting often continued. The tenacity with which fighting may be pursued is illustrated by the following incident:

> *5 June 1975, 1830 h*. Two birds (A & B) are present in a small crack at N. The bird on the outside (B) is attacked four times

> by a third bird (C), which lands beside it and grapples it by the bill and drags it off the ledge. Each time that B returns it is greeted by A in the usual manner and within a few seconds attacked again by C. At the fifth attack (after my arrival) C apparently arrives first and tries to grapple A. B returns 3 s later and B and C fall off the ledge again locked together. Twice again C attempts to drag B off, but is repulsed each time. On the third attempt C pulls B off by a wing (1845 h). I leave at 1850 h, by which time neither of the opponents had returned. (AJG)

At 1100 h the next day, however, identical behaviour was in progress, so that intermittent hostilities may have been maintained over a period of at least 17 h.

While grappling with their bills, birds usually brought their bodies parallel to one another, so that when they beat their wings they struck their opponent on the back or flanks. They held their wings flexed and beat them very rapidly, striking with the carpal joint, which forms a hard surface; the effect on human knuckles is extremely painful. In prolonged fights the birds often beat their wings only intermittently, apparently resting at intervals. Some losers appeared completely exhausted by the end of an encounter, which indicates the severity of the punishment inflicted.

During regular observations on murre behaviour, we recorded the level of aggression by counting the number of fights observed, defining a fight as any aggressive interaction in which both the birds involved pecked one another. This excluded one-sided encounters where prospecting birds were driven off by site-holders without retaliating, because the frequency of this type of interaction was likely to be dependent on the numbers of prospectors present. The majority of fights recorded involved less than 10 pecks. Fights which included grappling with the bill were rare, particularly after the beginning of egg laying.

### 2.4. Departure

Birds departing from occupied sites often held their wings raised for several seconds before launching off the ledge. Birds could launch themselves directly from most sites, although in a few places they had to walk up to 1 m to do so. During the first 10 s of flight, the birds sometimes flapped their wings slowly and deeply and raised them higher than normal on the up-stroke. They held their bodies horizontally, with the legs dangling.

This display is called "butterfly flight" and has been described for this species (Pennycuick 1956) and for Razorbill *Alca torda* (Conder 1950).

A typical sequence for departing birds was to flap normally (2–3 s), butterfly flight (4–5 s), glide on arched wings (1–2 s), and then close their wings and dip their heads forward to plummet towards the sea. The departure of prospecting birds was not usually characterized by any stereotyped behaviour pattern.

## 2.5. Behaviour on the water

We made no quantitative observations on the behaviour of birds on the water at the foot of the cliffs, but social interactions were common. Tuck (1961) described a display which he named the "water dance", in which two birds (occasionally more) race across the surface of the sea, beating the water strongly with their wings, but without rising into the air. They often travel in circles or figures-of-eight, keeping within two or three body-lengths of one another and, after some distance, may dive beneath the surface and continue the pursuit under water. We saw this behaviour frequently at Prince Leopold Island during the pre-laying period and irregularly throughout the remainder of the season, particularly when the sea was calm.

Thick-billed Murres commonly congregate on ice pans floating at the foot of the colony cliffs (E. Greene)

# 3. Colony attendance

## 3.1. Pre-laying period

Observers arrived at Prince Leopold Island in time to see the first occupation of the cliffs only in 1976, when observations began on 5 May. A flock of 50–60 murres flew past the cliffs that day and another flock on 7 May. We first observed birds sitting on the cliffs at 1000 h on 12 May; 26 were present during the daily count. Probably this was the first landing at the colony that season.

We observed considerable activity from 18 May onwards, with birds flying along the cliffs and landing briefly. Large leads appeared in the ice immediately offshore on the east side of the island on 20 May and, from that date onwards, hundreds of murres were on the water whenever any birds were on the cliffs. Large numbers of murres first appeared on the cliffs on 23 May. During the early part of the pre-laying period, activity on the cliffs appeared to be higher in mid morning than at the time of the daily count (1700–1900 h).

The following is typical of behaviour displayed at this time:

> Individuals and small groups (5–10 birds), but mainly individuals, leave flocks on the water and make forays to the cliffs, some landing, most circling, leaving again. "Hundreds" flying about at the base of the cliffs, over the shore ice. (B. Dodge, 1630–1800 h, 20 May)

Several thousand birds were estimated to be on the water at the foot of the cliffs.

From 23 May onwards there were usually at least a few birds present on the cliffs, but numbers counted did not exceed the number of breeding sites on the study plots (828) until 3 June, when 1005 birds were present (Fig. 9). This was therefore the first date on which at least one member of every pair could have been present at the colony. Peak numbers during the pre-laying period were recorded on 13 June when the 1469 birds counted represented approximately 89% of the breeding population and constituted the highest count of the year.

In 1975 only plots G1 and G4 were counted regularly during the pre-laying period; the highest count of 171 birds, recorded on 20 June, represented 76% of the breeding population. In 1977 numbers attending the colony prior to laying were lower, with a maximum count of 796 birds on the 10 study plots (Fig. 9), representing only 48% of the breeding population. In fact all of these counts probably include a few non-breeding birds and a number of sites where both members of the pair were present, so that occasions when all sites are simultaneously occupied during the pre-laying period must be relatively rare.

Departures of birds during pre-laying fluctuations were highly synchronized, with numbers falling from a peak to only a few birds within 12 h on several occasions. Behaviour during a period of build-up was monitored on 1–2 June 1976 at plot S1; using time-lapse cine photography (Fig. 10). From 0900 to 2400 h there were never more than two birds present on the plot at once, but at least 19 arrived.

The time spent on the plot by individual birds could be estimated because ledges were covered in fresh snow so that birds that shifted their position after arrival left visible tracks. The median duration was 5 min (range < 1–56 min). Later, when more birds were present, it was impossible to keep track of individuals, but the length of time spent by each bird probably increased, as judged from the apparent rate of new arrivals.

To assess the suitability of the study plots for monitoring fluctuations in the numbers of birds attending the entire colony, we counted birds on 13 days from 23 May to 20 June 1976 on a much larger area at G, including parts of the cliff much farther below the top than any of the study plots (Fig. 11). Numbers fluctuated synchronously throughout the period, although prior to 31 May a much smaller proportion of birds was present on the study plots than on the control area. After 1 June the two counts fluctuated together very closely and counts made on the study plots were representative of the entire colony.

**Figure 9**
Daily counts of birds on study plots made between 1700 and 1900 h during the prelaying period in 1975–77. Counts for 1975 are for plots G1 and G4 only. Those for 1976 and 1977 are for plots G1, G4, M, N, Q1, Q4, S1, S2, S3, and U

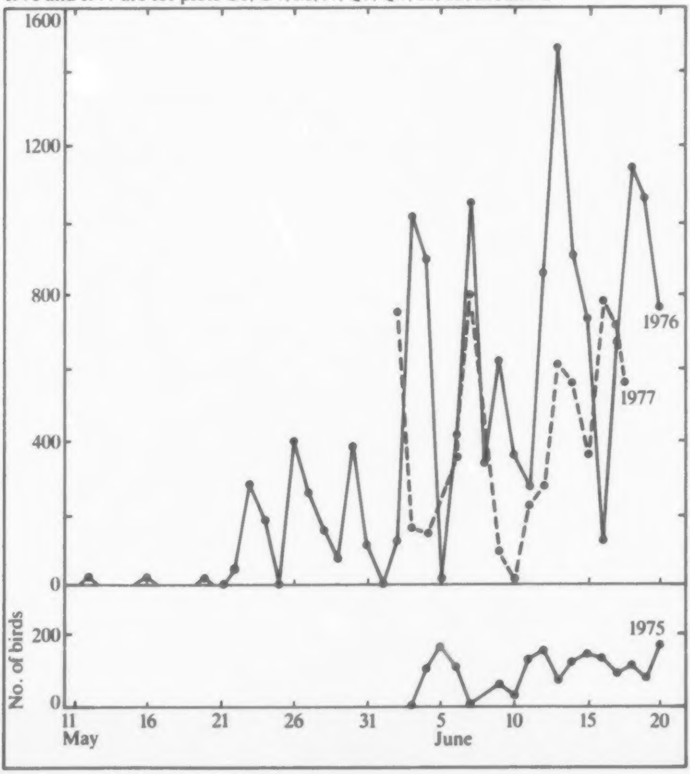


**Figure 10**
Counts of birds made from a time-lapse cine film showing the build-up in numbers at plot S1 between 1700 h 1 June and 0900 h 2 June 1976

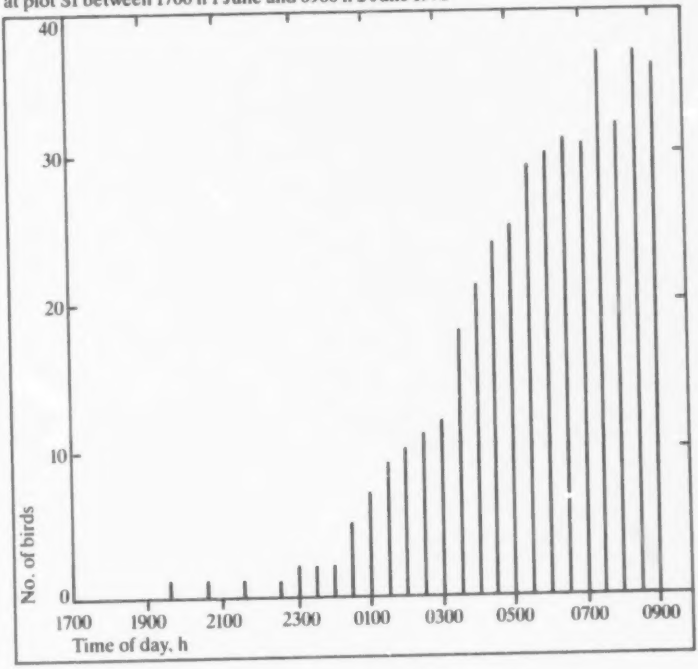
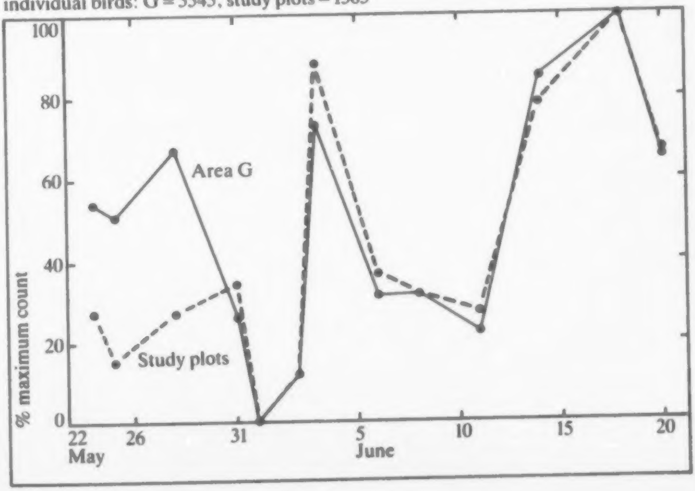


**Figure 11**
Comparison of counts of birds made on the study plots with those made on a much larger area at G during the pre-laying in 1976. Counts are expressed as percentages of the maximum counts, both of which occurred on 18 June. Maximum counts of individual birds: G = 5545, study plots = 1363

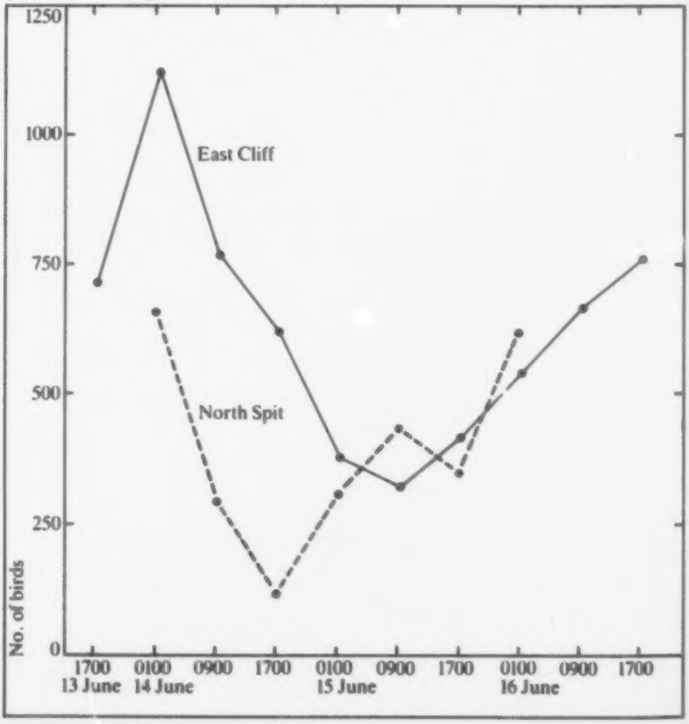


On 11 June we counted birds at all study plots every 2 h from 0000 to 2200 h; the totals varied from 126 to 527 birds. To test the degree of synchrony between different plots, Spearman rank correlation coefficients were calculated comparing the counts made at each site with those from every other site (App. 5). All pairs of plots were positively correlated in their fluctuations, but the degree of correlation between plots was not related to the distance between them. Hence, plots close together on the colony were not more closely correlated in their fluctuations than those farther apart.

In 1977, we compared the synchrony of attendance patterns at the East Cliff and North Spit colonies on 14 and 15 June. Five plots were counted at the North Spit colony, while the usual plots were monitored on the east cliffs. Numbers fell at both colonies until 1700 h on 14 June, but then rose on all plots at the north spit, while continuing to fall at 10 of 12 plots on the east cliffs until 0900 h on 15 June (Fig. 12). Weather conditions did not change significantly during the period. This comparison suggests that there was less synchrony between the two colonies than between different plots on the east cliffs.

In 1976 attendance during the early part of the pre-laying period appeared to be dependent on wind speed, numbers present

**Figure 12**
A comparison of changes in numbers of birds on the East Cliff and North Spit study plots over a 48-h period, June 1977



between 21 May and 5 June being inversely correlated with wind speed at 1900 h ($r_s = -0.88$, $P < 0.01$). Considering the latter half of the pre-laying period, from 1 June onwards, however, the effect of weather conditions on attendance seemed to vary. In 1975 we found no significant relationship between counts at G1 and G4 and any of the weather variables recorded, but in 1976 counts were inversely correlated with wind speed ($r = -0.435$, $P < 0.05$) and positively correlated with the change in barometric pressure over the previous 24 h ($r = 0.506$, $P < 0.05$). In 1977 fog obscured some plots during five counts, but if we consider only plots G1 and G4, where counts were possible every day, then similar relationships exist (wind speed, $r = 0.561$, $P < 0.01$; change in pressure, $r = 0.623$, $P < 0.01$).

A multiple linear regression analysis of counts at G1 and G4 in relation to wind speed at 0700 and 1900 h, barometric pressure at 1900 h, change in barometric pressure and wind speed over the previous 24 h ($\log_{10}$ transformed), visibility, and date, showed that 56% of the observed variation was explained by change in barometric pressure alone, with date explaining a further 10% and wind speed 8%. Only date showed a significant correlation when a similar analysis was performed for counts from all plots, omitting days affected by fog.

Both Corkhill (1971) and Birkhead (1978*a*) found that wind speed affected attendance patterns of Common Murres at Skomer Island, Wales, during the pre-laying period, but neither investigated the effects of barometric pressure.

### 3.2. Incubation and chick-rearing periods

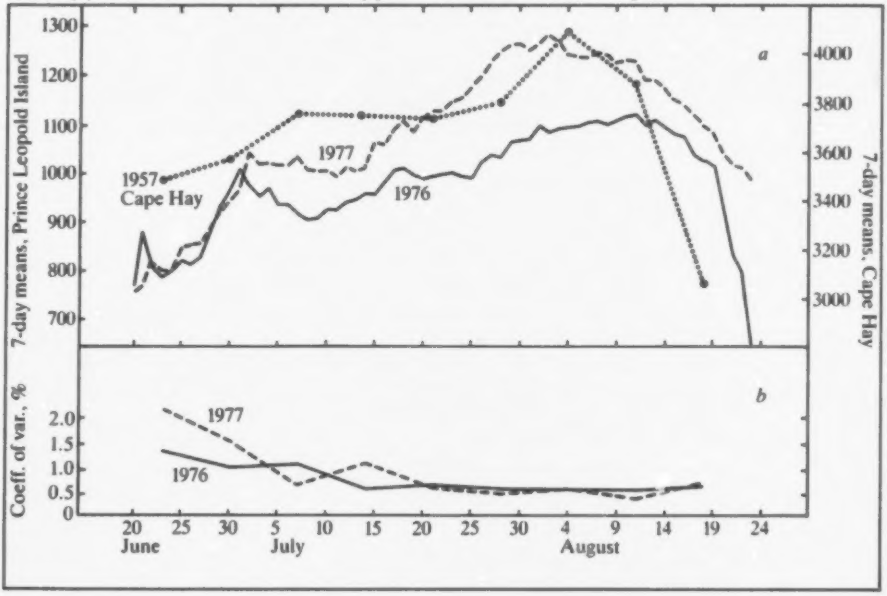
From the beginning of egg laying to the start of fledging most sites were permanently occupied by one member of each breeding pair. In all 3 years of our study daily counts never fell below the total number of breeding pairs from the median date of laying until late August (earliest date: 23 August 1976).

In both 1976 and 1977 numbers increased rapidly to a peak about 1–2 July, just after the median date of egg laying (Fig. 13). In 1976 they then fell until 9 July, rising steadily thereafter to a peak on 11 August, although a minor peak was also discernible on 18 July. In 1977 numbers remained relatively stable during 1–14 July, falling slightly, and then rose rapidly to a peak on 2 August, although a minor peak was again noticeable on 18 July. The minor peaks about 18 July in both years coincided with the appearance of large flocks of murres, probably a late wave of non-breeders, flying back and forth along the colony without landing. We observed similar behaviour about 16 July in 1975.

In 1976 numbers fell sharply after 19 August, when about 50% of chicks had fledged, but in 1977 the departure from the cliffs was more gradual. By 1 September in both years, however, the majority of birds on the cliffs during daily counts were brooding chicks. The pattern of attendance observed at plots G1 and G4 in 1975 was similar to those seen in 1976 and 1977, and all three resemble the pattern of attendance at the Thick-billed Murre colony near Cape Hay, Bylot Island, on a similar latitude (Fig. 13; Cape Hay data from Tuck 1961, but note that his counts were maxima of several daily counts).

Some important attendance statistics from 1975 and 1976 seasons are similar while 1977 data are "atypical", particularly in the

**Figure 13**
(*a*) Daily counts of birds at all plots on Prince Leopold Island in 1976 and 1977 smoothed as 7-day running means and 7-day means derived from counts made by Tuck (1961: App. C) in 1957 at Cape Hay, Bylot Island. (*b*) Coefficients of variation for 7-day periods for counts at Prince Leopold Island



numbers attending the colony during the pre-laying period and the early date of peak numbers during the chick-rearing period (Table 3). With such a small sample, however, the possible range of inter-year variation must remain a matter for conjecture.

A small bias is inherent in the figures collected for Prince Leopold Island, because on a few days fog prevented counting at some plots. Numbers were generally low at plots that could be observed on foggy days. During July 1977, six counts at plots S1, S2, and U, on days when other plots were obscured, were an average of 9.9% lower than the 7-day means for the same dates. The lack of counts for all plots on days when visibility was poor may have biased the figures used in Figure 13 upwards slightly.

Another, and more serious, weakness of the method used at Prince Leopold Island is the fact that peak attendance varies with time of day and that the daily peak shifts during the course of the season. During incubation, numbers tend to be highest at about 0800 h, but during the chick-rearing period the daily peak shifts to about 1800 h, although a second, lower peak at 0800 h persists (see this chapter, section 3.3). Because daily counts were made throughout the season at 1800–1900 h, they gradually came to approximate the daily maximum as the season progressed. The effect is fairly small, but if the diurnal pattern observed at plot S1 is representative, peak numbers during early July were probably about 6% higher than those recorded during the daily counts. A correction for this would have the effect of decreasing the apparent rate of increase during July.

**Table 3**
Comparison of some important attendance statistics 1975–77. Statistics for 1975 are based on study plots G1 and G4, and those for 1976 and 1977 on plots G1, G4, M, N, Q1, Q4, S1, S2, S3, and U

| | 1975 | 1976 | 1977 |
|---|---|---|---|
| Birds first seen on the cliffs | —* | 12 May | —* |
| 50% of breeders first present | 5 June | 3 June | 16 June |
| Peak no. during pre-laying (as % of breeders) | 76% | 89% | 48% |
| Date after which no. of birds did not fall below no. of breeding pairs | 21 June | 25 June | 28 June |
| Date of peak 7-day mean | 13 Aug. | 11 Aug. | 2 Aug. |
| Peak 7-day mean as % of breeders | 76% | 70% | 79% |
| Date when count of birds first fell below the no. of breeding pairs | 24 Aug. | 23 Aug. | 27 Aug. |
| Last bird seen on the study plots | —† | 7 Sept. | —† |

* Birds were present when investigators arrived.
† Small numbers of birds were still on plots at camp closure.

**Table 4**
Differences between mean counts of birds made at seven plots from 1–8 August in 1976 and 1977

| Study plots | Mean no. of birds | | % difference |
|---|---|---|---|
| | 1976 | 1977 | |
| G1 | 77.50 | 86.29 | 11 |
| G4 | 92.87 | 105.86 | 14 |
| N | 153.62 | 165.57 | 8 |
| Q1 | 161.25 | 196.71 | 22 |
| Q4 | 105.36 | 120.29 | 14 |
| S1 | 228.12 | 263.71 | 16 |
| U | 87.50 | 93.57 | 7 |

Differences in counts between 1976 and 1977 held for all plots (Table 4). The difference was greatest on plot Q1, where mean numbers during 1–8 August were 22% higher in 1977 than in 1976, and smallest at plot U, where numbers were only 7% higher. It may be significant that at plot U most ledges are very small, with little room for prospecting birds to land without being attacked by sitting birds, whereas plot Q1 includes several unoccupied ledges and broad platforms where prospectors can land easily. Plot Q1 also exhibited a greater than average change in numbers during the course of the season, increasing by 91% between 20 June and 1 August 1977. The adjacent plot, Q4, comprising mainly two very densely packed ledges, increased by only 48% during this period (Fig. 14).

Day-to-day variation in counts fell during June and July in all years, reaching a minimum in mid August (Fig. 13). To measure variability we calculated the coefficient of variation over 7-day periods to compensate for changes in the mean number of birds present with season. A comparison of seven plots shows that for the period of minimum variability (1–8 August), coefficients varied from 5.23% (plot U) to 9.44% (plot G4).

To examine the effect of increasing sample size on the coefficient of variation, the statistic was calculated for successive combinations of plot 1, 2, 3 . . . 9, ranked from south to north along the East Cliff colony. Variation decreased with increased sample size (Fig. 15), presumably because of the dilution of local effects. The resulting points can be fitted to a log curve, which predicts a coeffi-

**Figure 14**
A comparison of the seasonal variation in counts of birds at plots Q1 and Q4, both on the same cliff and only about 80 m apart. Means are plotted for each 7-day period as percentages of the mean for the period 17–23 June 1977

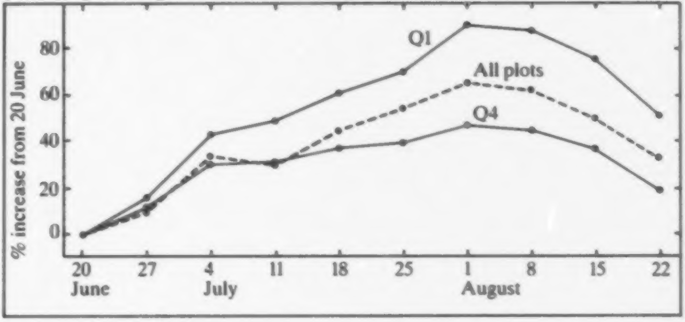
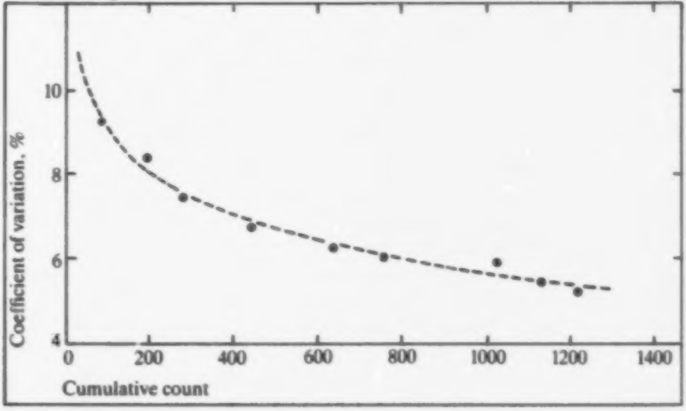


**Figure 15**
The relationship of sample size to coefficient of variation for counts of birds made during 1–8 August 1977. Plots were summed in order from south to north along the cliffs, starting with G1. The dotted line shows the fitted curve, $y = 16.01 - 1.50 \ln x$



cient of 5.65% for a mean of 1000 birds counted. This suggests that over a week of replicate counts during early August, the 95% confidence limits on the mean should be about 5% (SD = 56.5, $N = 7$, $t = 2.365$) and indicates that 1000 birds may be a suitable minimum sample size for population monitoring. No evidence was found of regular oscillations over several days, as was detected for Northern Fulmars on Prince Leopold Island (Greene and Nettleship 1981).

To analyse the effect of weather conditions in determining observed fluctuations in daily counts during the incubation and chick-rearing periods we used "d", the amount by which the daily count differed from the 7-day mean. An analysis of data from all daily count plots for 1976 suggested that the presence or absence of fog, as measured by visibility estimates, had a significant effect on the numbers of

**Table 5**
The effect of visibility on "d" in 1977*

| | Visibility | | | |
|---|---|---|---|---|
| Year | < 400 m | ≥ 400 m | *t* | *P* |
| 1976 | − 9.58 (7) | −0.51 (47) | 1.67 | 0.1–0.2 |
| 1977 | −33.67 (12) | +9.05 (41) | 2.45 | 0.018 |

* Values in parentheses are sample sizes.

**Table 6**
Correlation between mean counts of birds at plot S1 during watches every 3 days, 25 July – 21 August 1977 inclusive, and wind speed and visibility

| | Correlation coefficients | |
|---|---|---|
| Weather variable | Incl. 19 August | Excl. 19 August |
| Wind speed | −0.85* | −0.51 |
| Visibility | −0.57† | −0.10 |
| *N* | 12 | 11 |

* $P < 0.01$.
† $P < 0.05$.

birds present. On days with very dense fog some plots could not be counted and daily counts were therefore incomplete. To avoid any bias due to the omission of these days, we limited analyses of counts in relation to weather to plots S1, S2, and U, which were sufficiently close to the observation points that fog did not affect the counts. For 1977, we also analysed the means of counts made during 4-h watches.

Simple correlation analyses of "d" in relation to all weather variables, for counts at S1, S2, and U in 1977, did not reveal any significant associations. In 1977 visibility was positively correlated with "d" and explained 7.3% of the variability. A comparison of days with visibility estimated at < 400 m with days of better visibility also demonstrated a significant effect (Table 5), and a similar insignificant effect was apparent in 1976. A step-up multiple regression analysis of "d" in relation to all weather variables for plots S1, S2, and U showed that only 11% of the variation in 1976 and 8% in 1977 could be explained by weather conditions.

In 1977 mean counts made during 4-h watches at S1 were significantly correlated with wind speed and visibility (Table 6), although these correlations were no longer significant when the watch made on 19 August, during the worst gale and snow blizzard of the season, was omitted. A step-up multiple regression analysis showed that visibility did not add significantly to the amount of variation explained by wind speed (72%). Considering all of these results we conclude that weather is not usually important in determining attendance at the colony during the incubation and chick-rearing periods, but may have a marked effect when conditions are extreme.

### 3.3. Diurnal variation in attendance

Counts made every 2 h over 24 h at all plots on 11 and 29 July 1976, during the incubation period, showed no comparable pattern of diurnal fluctuations in attendance, with a single peak occurring at 1800 h on 11 July and two peaks at 0600 and 1600 h on 29 July (Fig. 16). Means of counts made at plot S1 every 2 h during 24-h watches in 1975, however, show a weak diurnal pattern, changing from a peak in the middle of the day during the incubation period to a peak at 1800 h during the chick-rearing period (Fig. 17).

The mean diurnal count at plot S1 in 1975 fluctuated between 163.2 and 185.8 birds during incubation (13.8% of the minimum) and between 176.8 and 193.2 birds during chick rearing (9.3% of the minimum). During incubation variation was lowest when total numbers were low, at midnight and 0200 h, and high in the middle of the day; but during the chick-rearing period no recurrent pattern of variation with time of day was apparent (Fig. 17). Coefficients of variation calculated for all counts made during each 24-h watch showed that diurnal variation was lowest between 22 July and 3 August, the first half of the chick-rearing period (Fig. 18). Variation increased rapidly after 19 August, with the pattern of two peaks becoming most marked just before the majority of birds left the colony (24 August) (Fig. 19).

**Figure 16**
Counts of birds made every 2 h at all plots and at S1 only on 11 and 29 July 1976

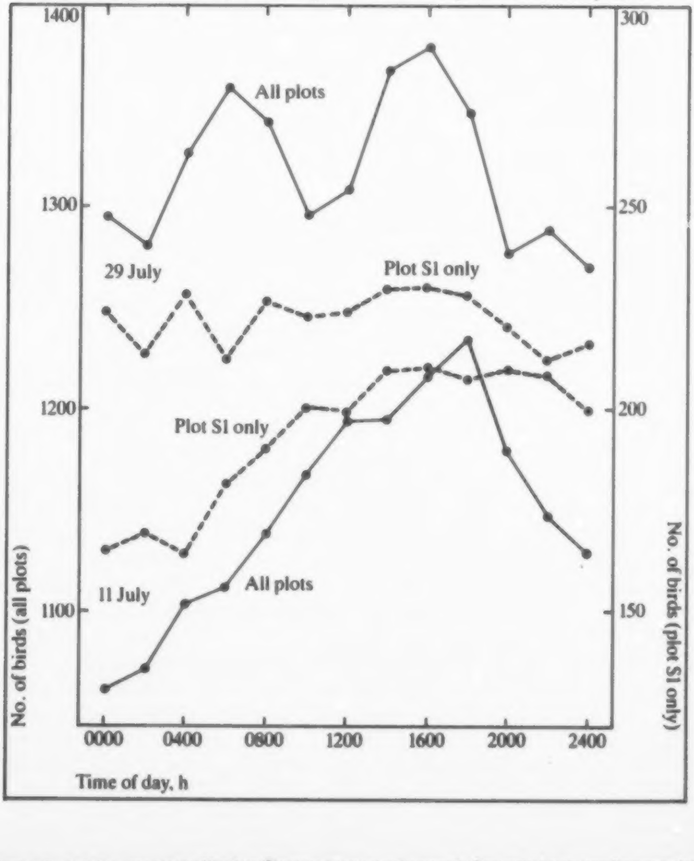


**Figure 17**
Means of counts of birds made every 2 h on (*a*) six watches during the incubation period and (*b*) five watches during the chick-rearing period at plot S1 in 1975. Dashed lines show coefficients of variation for the means

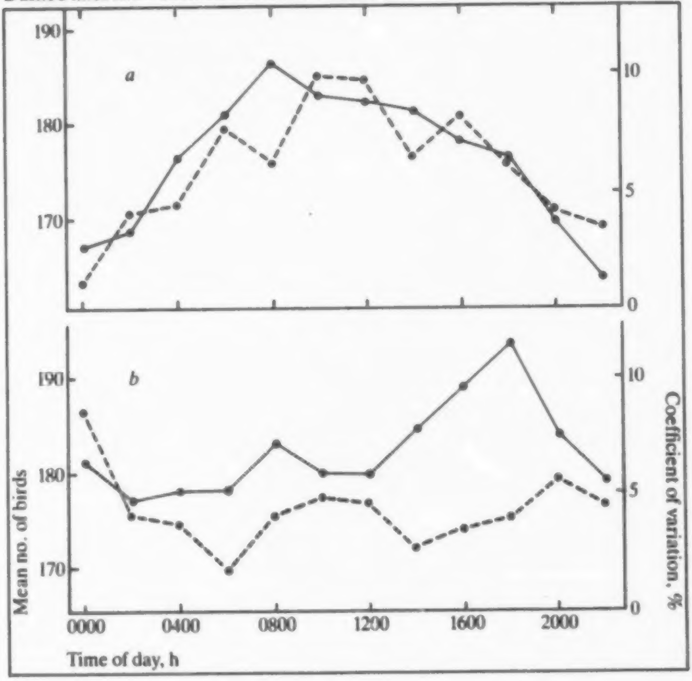


**Figure 18**
Coefficients of variation for counts of birds made every 2 h over a 24-h period on 11 watches at plot S1 during 1975

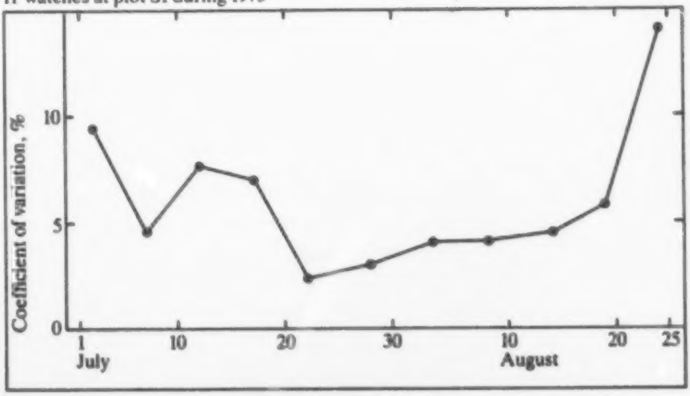
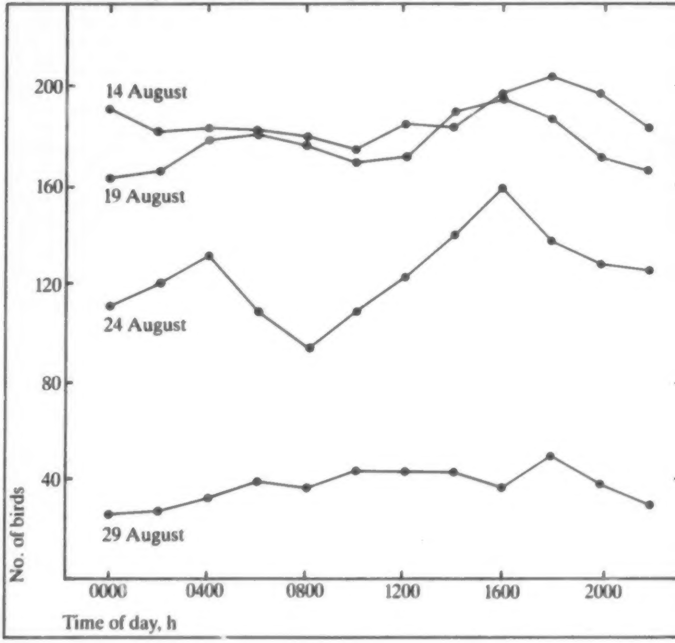


**Figure 19**
Numbers of birds present on plot S1 during the last four 24-h watches in 1975



The degree of synchrony between plots in fluctuations occurring over 24 h was lower during incubation than during the pre-laying period. Appendix 6 gives a correlation matrix of Spearman rank correlation coefficients for all plots counted every 2 h on 11 July 1976. Eighty percent of correlations were positive, but only 18% were significant at $P < 0.05$ and the overall degree of synchrony was rather low, with a median correlation coefficient of 0.3. As in the pre-laying period, adjacent plots were not more synchronized than those farther apart.

### 3.4. Attendance patterns and population monitoring

Seabird census techniques and the interpretation of the resulting statistics vary with the purpose for which they are intended. The most satisfactory statistic, ideally, is the total number of birds comprising a discrete population on a given date, but in practice it is rarely possible to achieve this. For some seabirds, we can enumerate the breeding population by counting the number of occupied nests; but in the case of murres, which build no nest, the best that can normally be achieved is a count of the total numbers of birds present at the colony (Lloyd 1975, Nettleship 1976, Birkhead and Nettleship 1980).

For censuses intended to monitor changes in populations from year to year in relation to environmental changes induced by human activity, it is important to know the level of natural variation likely to be encountered. The extent to which counts made in different years can be compared will depend on the following factors, which are themselves likely to be interrelated:

(1) how closely the timing of observations conform between the two years (date, time of day),
(2) differences in the phenology of breeding between the two seasons,
(3) differences in weather conditions between the seasons,
(4) changes in the size of the non-breeding population due to between-year variations in recruitment (annual productivity), and
(5) differences in the relative abundance of food.

Comparisons of within- and between-day variation in counts over the season suggest that for Thick-billed Murres at Prince Leopold Island counts are most likely to be replicated in the middle of the chick-rearing period (early August). Lloyd (1975) reached a similar conclusion regarding censuses of Common Murres and Razorbills on Skomer Island, Wales. At Prince Leopold Island the time of day chosen at this point in the breeding cycle has little influence on variability, although it may be best to avoid the period of the daily peak at 1400–1800 h (unfortunately, the time we chose initially at Prince Leopold Island). Provided that counts are conducted on days when visibility exceeds 400 m and wind speed is below 30 km/h, weather conditions should also have relatively little effect.

Mean counts derived from replicate counts made over several days are more comparable than single counts, although averaging is less effective when numbers are increasing, during July, than after they have stabilized in August. The relationship of the standard error of the mean to the number of days of consecutive counts in July and August 1977 suggests that the accuracy of estimation improves substantially by repeating counts for up to 12 days, but continuing counts beyond that time reduces the standard error only a little (Fig. 20). Ninety-five percent confidence limits for the mean over the first 12 days of July were 11.4% ($\bar{x}$ = 1040.64) and for the first 12 days of August, 5.3% ($\bar{x}$ = 1274.58). Given that dates and times are replicated, therefore, and no extreme weather conditions are included, counts of about 1000 birds replicated over 12 days in early August could be expected to reveal a 5% difference between years. The question then is whether a statistically significant change of this magnitude probably represents a real change in the size of the population, or a naturally occurring inter-year variation determined by factors 2, 4, and 5 above.

A more sensitive method for testing differences among counts made in different years would be to test paired observations, using counts either made on the same date in different years, or indexed to events in the breeding cycle, possibly the median date of laying. This method removes variation due to seasonal trends, giving a smaller standard error and hence a greater ability to detect statistically significant differences between years. Table 7 shows that the standard error of the mean difference between paired observations is lower than the standard error of the difference between the means for two sample periods.

We cannot give even approximate confidence limits for inter-year variation on the basis of data collected at Prince Leopold Island. The difference of about 10% between counts made in July and August

**Figure 20**
Relationship between the number of days of replicate counts and the standard error of the mean, beginning from 1 July and 1 August 1977. Curves are fitted by eye

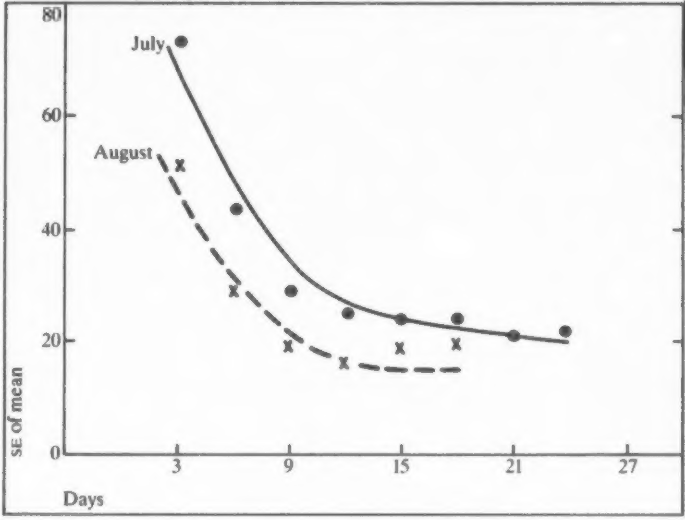


**Table 7**
Comparison of standard errors calculated for the difference between mean counts over two periods in 1976 and 1977 and the standard errors calculated for mean differences between paired observations on the same dates

| | Year | | Difference between paired |
|---|---|---|---|
| Period* | 1976 | 1977 | counts ($1/n\Sigma d_i$) |
| 20–31 July | | | |
| mean ($n = 12$) | 1047.67 | 1222.58 | 174.91 |
| SE | 32.59 | | 23.56 |
| 1–12 August† | | | |
| mean ($n = 10$) | 1144.0 | 1272.0 | 128.0 |
| SE | 26.62 | | 17.53 |

* SE of mean difference $= \sqrt{\frac{1}{n(n-1)} (\Sigma d_i^2 - n\bar{d}^2)}$

SE of difference between means $= \sqrt{\frac{1}{n(n-1)} \left[ (\Sigma x_i^2 - n\bar{x}^2) + (\Sigma y_i^2 - n\bar{y}^2) \right]}$

where $x$ and $y$ are counts made on successive days in 1976 and 1977 and $d$ is the difference between paired counts ($y_i = x_i$).

† One count is missing in each year for this period.

in 1976 and 1977, when numbers of breeding pairs on the study plots were almost identical (see Chapter III, section 2), suggests that a change in mean numbers over 10 counts of at least 15% is necessary before a change in the size of the breeding population is implied. Changes occurring in the same direction over a number of years would probably constitute more reliable evidence of an underlying population trend. Most of the difference between counts in 1976 and 1977 is probably accounted for by differences in the number of prospectors visiting the colony (see this chapter, section 4), which is presumably determined by the abundance of food supplies. Monitoring rates of arrival of prospecting birds at the same time should indicate whether this factor is contributing to observed differences between counts in different years, although the quantitative relationship between rates of arrival and counts will vary both within and between colonies.

Recommendations for counting procedures to be used in monitoring populations of Thick-billed Murres are as follows:

(1) visit the colony for about 10 days during the period between the end of egg laying to the first fledging;

(2) select and accurately define (map and photograph) about 10 study plots scattered throughout the colony and include all types of breeding ledges — each plot should contain about 100 individual birds (equivalent to 70–80 breeding pairs);

(3) count each plot daily at the same time, about mid day; and

(4) conduct watches at one or two of these plots for several hours each day at the same time to determine rates of arrival of prospectors and feeding rates for chicks.

Complete details of methods are presented in Birkhead and Nettleship (1980).

The time of day may be more crucial at colonies farther south than Prince Leopold Island, where changes in light intensity, particularly in August, may make the daily fluctuations much greater. Tuck (1961) found at Akpatok Island that both members of the pair were on the cliffs throughout the night in August and under these conditions a late evening or early morning count might yield the most consistent results.

Patterns of attendance for the Common Murre appear to be rather different from those observed for the Thick-billed Murre at Prince Leopold Island. At Skomer Island, Wales, Birkhead (1978*b*) found that off-duty breeders spent a far greater proportion of their time (20–40%) on the cliffs throughout the season than was observed for Thick-billed Murres. Consequently, the presence or absence of site-holders, rather than the behaviour of prospecting birds, mainly determines attendance statistics. As off-duty breeders spend the longest periods at the colony during the late incubation period, peak counts are also recorded at this stage and not, as was the case at Prince Leopold Island, during chick rearing. The difference probably has little effect on census procedures. At Skomer Island only one member of each Common Murre pair remained on the cliffs at night and hence very early morning counts were the most reliable.

# 4. Behaviour

## 4.1. Behaviour during the pre-laying period

Behaviour during the period up to the laying of the first egg was considerably affected by the great fluctuations in the numbers of birds at the colony. When numbers were small, individuals were usually well spaced out and there was little opportunity for social interaction. The peak numbers recorded during the pre-laying period, however, were the highest for the season and hence the breeding ledges were the most crowded during this period.

**Figure 21**
Rates of copulation and attempted copulation observed during the pre-laying and early incubation periods

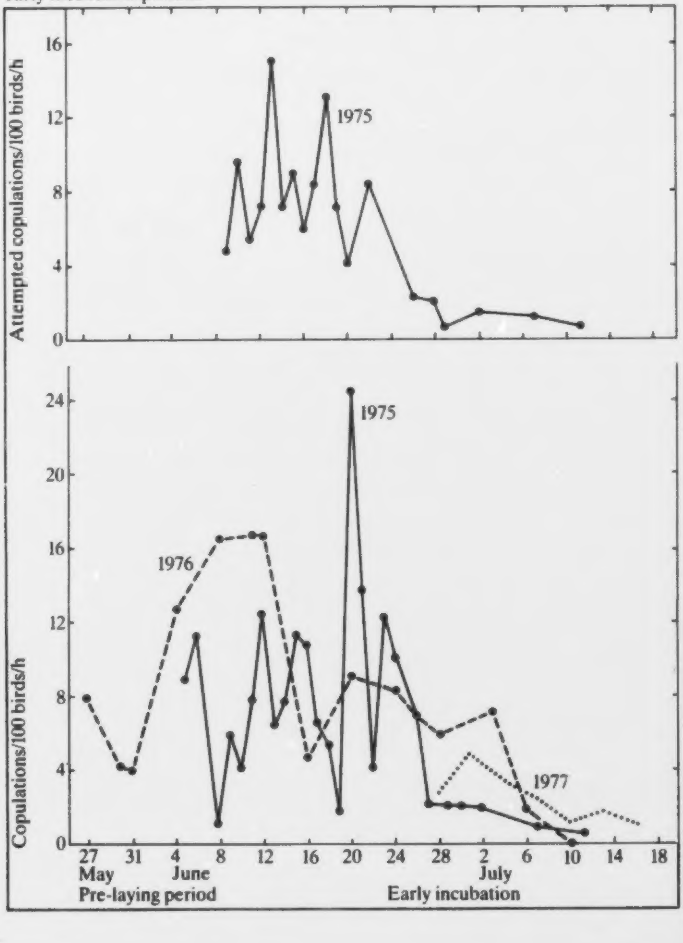
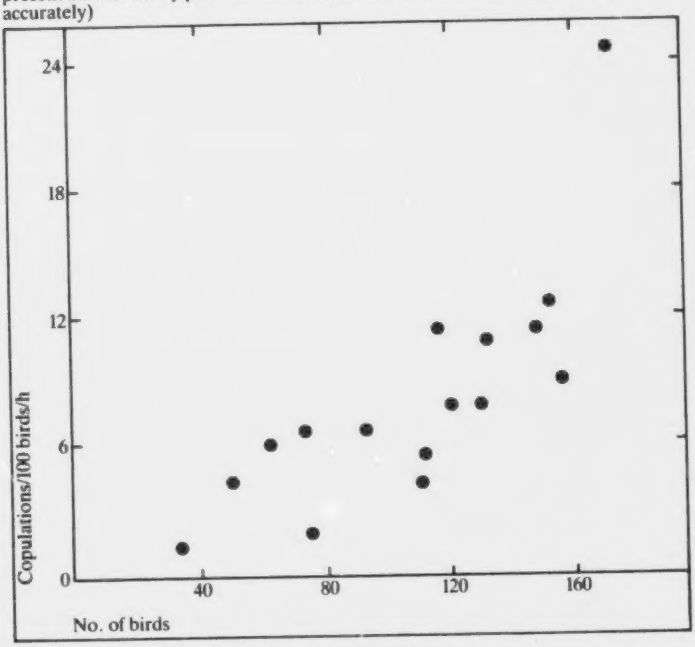


**Figure 22**
Rates of copulation observed at plot G3 in 1975 in relation to the number of birds present on the nearby plots G1 and G4 (plot G3 itself was difficult to count accurately)



Copulations were observed on the nesting ledges throughout the pre-laying period, but at plot G3, where the frequency was recorded from 5 June in 1975 and from 27 May in 1976, the rate of copulations was highest in the last 3 weeks before egg laying began (Fig. 21). Maximum rates of copulation observed were 24.6/100 birds/h in 1975 and 16.8/100 birds/h in 1976, representing mean intervals between copulations for individual pairs of 2 and 3 h respectively.

Copulations were never observed at sites where an egg was present and the overall rate of copulations, therefore, declined as soon as egg laying commenced. In 1975, the year for which the most data were available, we found a strong correlation between the rate of copulation during the pre-laying period and the number of birds present (Fig. 22).

Attempted copulations were recorded from 9 June onwards in 1975. Casual observations earlier in the season suggested that this behaviour was unusual before 9 June. Peak rates of attempted copulation occurred during the pre-laying period, but daily rates showed no significant correlation with rates of copulations ($r = 0.414$, $N = 13$, $P > 0.05$). The ratio of successful to attempted copulations was significantly correlated with the number of birds present ($r = 0.582$, $N = 13$, $P < 0.05$), which suggests that attempted copulations were relatively more likely to occur when few birds were present.

**Table 8**
Sex of birds involved in copulations or attempted copulations immediately after landing, in relation to time of day during the pre-laying period in 1975

| | Copulation* | | | Attempted copulation | | | Number of arrivals followed by copulation |
|---|---|---|---|---|---|---|---|
| Time, CDT | *N* | Male | Female | *N* | Male | Female | |
| Before 1200 h | 24 | 15 | 9 | 8 | 7 | 1 | 32 |
| After 1200 h | 114 | 96 | 18 | 14 | 10 | 4 | 128 |
| Totals | 138 | 111 | 27 | 22 | 17 | 5 | 160 |

* Testing sex ratio in relation to time of day, $\text{chi}^2 = 5.94$, $P < 0.02$.

Copulations and attempted copulations frequently occurred within a few seconds of the arrival of one of the participants and this enabled us to identify the sex of the arriving bird. Reverse copulations were not seen in observations on marked pairs. During the pre-laying period in 1975, 80% ($N = 138$) of the arriving birds involved in copulations were male, as were 74% ($N = 22$) of those involved in attempted copulations. There was some indication from these records that the proportion of the sexes among birds arriving at the colony varied with time of day, with females forming a higher proportion in the morning than in the afternoon (Table 8). Further evidence for differences between the sexes in their schedules of attendance at the colony comes from birds collected flying towards the colony. Out of 23 collected between 1200–1300 h on 23 May and 4 June 1976, 17 were males ($P = 0.017$, binomial test).

The incidence of fighting during the pre-laying period in 1975 and 1976 at plot G3 was highest during the last 10 days before egg laying, with maximum rates of fighting of 16.8 fights/100 birds/h in 1975 and 25.2 fights/100 birds/h in 1976 (Fig. 23). After the start of egg laying, rates of fighting fell in both years and in 1976 did not exceed 20 fights/100 birds/h again until August. Surprisingly, no significant correlation was found between the incidence of fighting and the number of birds present ($r = 0.268$, $N = 16$, $P > 0.1$), but a significant positive correlation was found with the rate of arrivals at the plot (Fig. 24).

Unfortunately we did not observe aggressive behaviour when birds first arrived at the colony, the first systematic watch in 1976 being carried out on 27 May. Up to that date the maximum daily count had been less than 50% of the eventual number of breeding pairs, and many sites were probably still not occupied. Rates of fighting in excess of 20 fights/100 birds were recorded only after 3 June, when the daily count exceeded the number of breeding pairs. In 1975 the pattern of fighting suggested a period of maximum overt aggression between 10 and 17 June, presumably as site-holders consolidated their right of possession. A similar, though less clear, pattern can be discerned for 1976.

There was no diurnal pattern in the incidence of fighting during two round-the-clock watches conducted in the pre-laying period in 1975. Rates of fighting recorded in 1975 and in 1976 differ possibly because different observers were involved, but within-year comparisons should not be affected.

**Figure 23**
Frequency of fighting during the pre-laying periods in 1975 and 1976

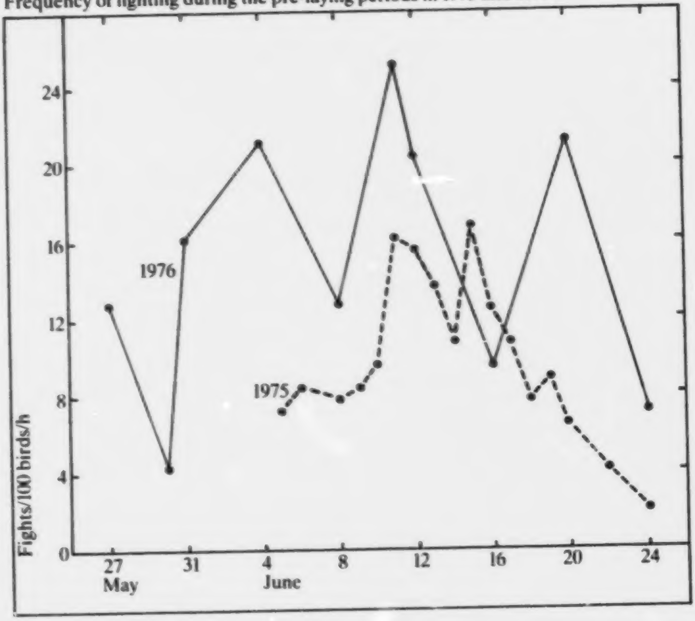
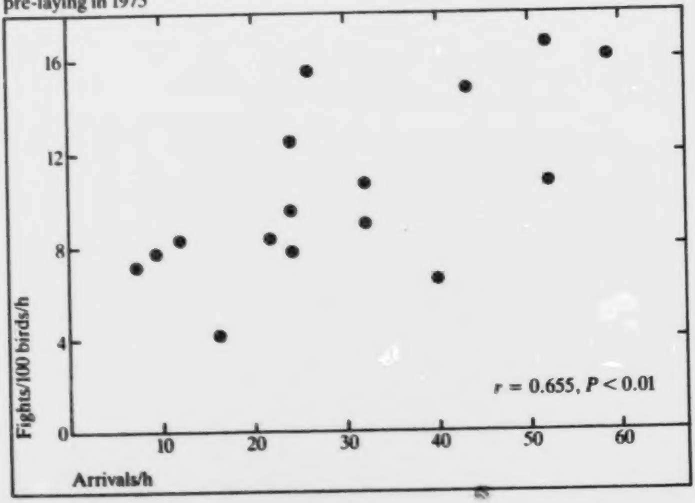


**Figure 24**
Frequency of fighting in relation to the number of birds arriving on plot G3 during pre-laying in 1975



## 4.2. Egg laying and incubation

We observed laying between 0945 and 1710 h ($N = 25$) but a diurnal peak is not necessarily indicated as our watches were concentrated at this time of day. Egg laying took 2–5 min during which time the female stood up, stretched her legs, and bent her tail under the body so that the cloaca was directed forward towards the cliff. For balance the bird leaned against a vertical rock face, if one was close by, or spread its wings, sometimes across the backs of adjacent site holders. The male was sometimes present during laying and on one occasion apparently prevented the egg from rolling off the ledge (B. Dodge), but this was not normal.

Copulation ceased once the egg had been laid. In a few cases males arriving just after the egg had been laid attempted to copulate, but were rejected by the female. The male's first spell at incubation was unusually long (ca. 48 h, Fig. 25), but thereafter incubation spells averaged not more than 24 h. The rate of exchanges of incubation duty increased as the season progressed, from about one per day in late June to two or more in late July and August (Fig. 26). After the first 4 days, the rate was not related to the time elapsed since laying and the effect, therefore, seems to be due to seasonal rather than developmental factors.

Arriving birds did not take over incubation immediately. The time elapsing between arrival and the exchange ranged from a few minutes to 1.5 h at plot S1 during 10 days in late July 1977 (Fig. 27) and the median interval increased from 1.5 min on 28 June to 11 min on 31 July (Fig. 28).

After an exchange, the bird that had been relieved usually flew away within a few minutes, normally exhibiting the butterfly flight for the first few seconds. Observations of birds leaving the cliffs made from the beach below the colony showed that in July most birds using the butterfly flight landed on the sea, whereas a high proportion of

**Figure 25**
Number of incubation changes observed in 24 h in relation to the time elapsed since egg laying at plot S1 on 2 July 1975

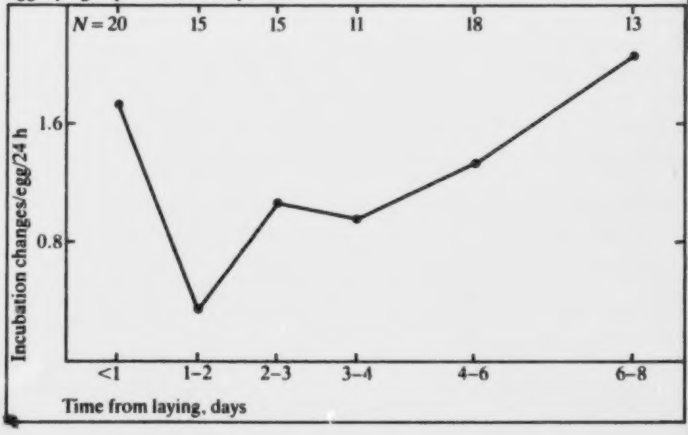


**Figure 26**
Number of incubation exchanges observed during 24-h watches in relation to date at plot S1 in 1975 and 1977

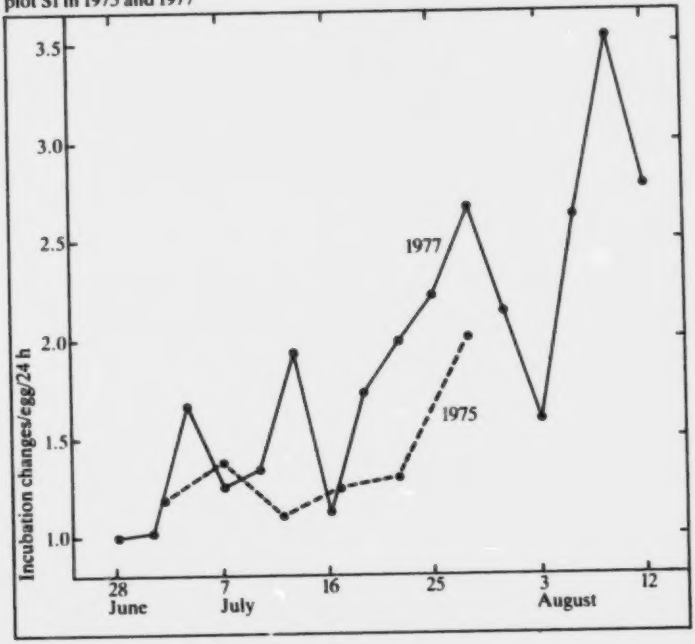


**Figure 27**
Time intervals between arrivals and incubation change-overs at plot S1, 22–31 July 1977

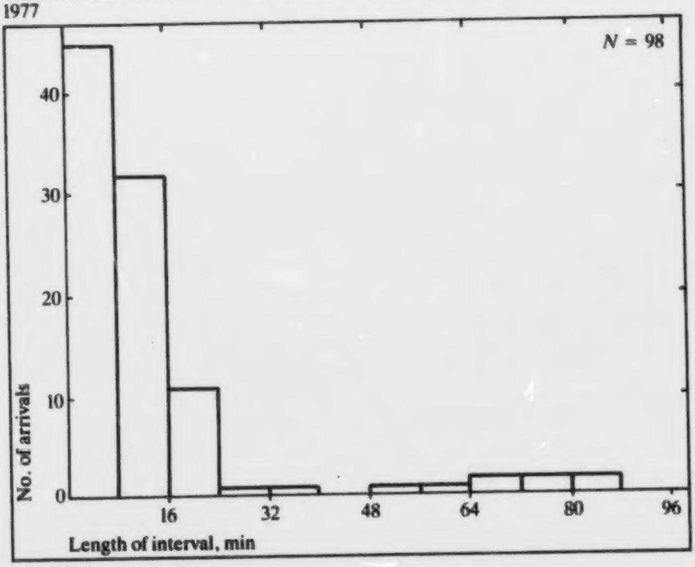
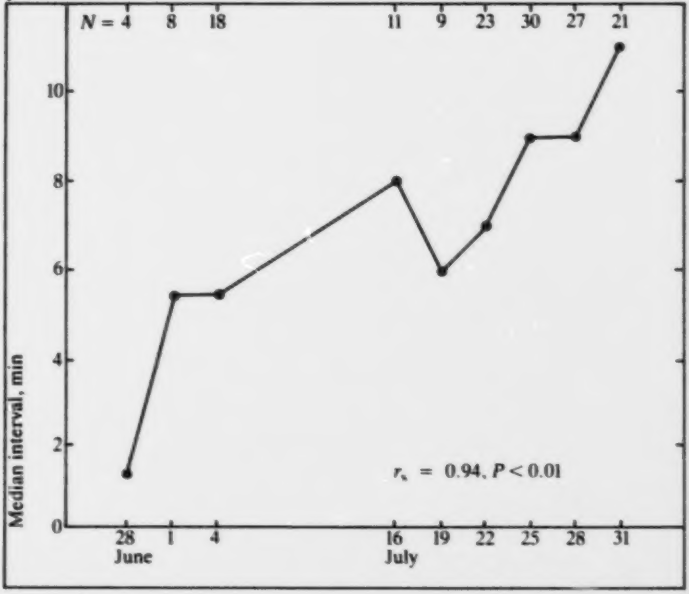


**Figure 28**
Median duration of time interval between arrival and exchange in relation to date at plot S1 in 1977



those which did not use the butterfly flight returned immediately to the cliffs (Table 9). The latter were presumably non-breeding birds. In Razorbills the butterfly flight frequently involves pairs, and occasionally three birds, flying close together (Conder 1950). The birds often circle and all return to a ledge together, indicating that the significance of this display may differ between the two species. The function of the display in the Thick-billed Murre is hard to understand because, in the majority of cases, the departing bird would not be visible to its mate once it had left the ledge.

Incubation exchanges occurred throughout 24 h and single watches did not reveal any pattern of diurnal variation, although there was a tendency for the rate of change-overs to be highest at 0600 and 1800 h. Collections of birds shot while flying towards the colony suggested that, as in the pre-laying period, the sexes maintained different schedules of attendance at the colony during incubation. Eleven out of 15 birds shot between 1000 and 1700 h on 15 July 1976 were males, as were all six birds shot on the same date at the same time of day in 1977 ($P$ = 0.12 and 0.03, binomial test), whereas the sexes were in equal proportions among 16 birds collected at 2200–2400 h on 30 June 1977.

Further evidence on the schedules of the sexes during incubation was provided by the pairs of known sex on plot U. We removed eggs from all five sites. Between that day and re-laying, males were present on 66% of site-days during daily counts (made between 1700 and 1800 h), presumably because the females were devoting most of

**Table 9**
Incidence of "butterfly flight" in relation to whether birds subsequently landed on the sea or not.* Watches made from the beach below the East Cliff colony on 19, 23, and 26 July 1977

| Behaviour at departure | Landed on sea | Did not land on sea | *N* |
|---|---|---|---|
| "Butterfly flight" | 10 | 2 | 12 |
| Normal flight | 16 | 35 | 51 |

* $Chi^2 = 10.82$ (with Yates' correction), $P < 0.01$.

**Table 10**
Attendance of marked pairs during the interval between the removal of their egg to re-laying (7–18 July) and after re-laying (22 July – 8 August) at plot U in 1977

| | Total site-days | | Binomial |
|---|---|---|---|
| Date | Male present | Female present | probability |
| 7–18 July | 29 (66)* | 15 (34) | 0.025 |
| 22 July – 8 August | 26 (25) | 76 (75) | 0.001 |

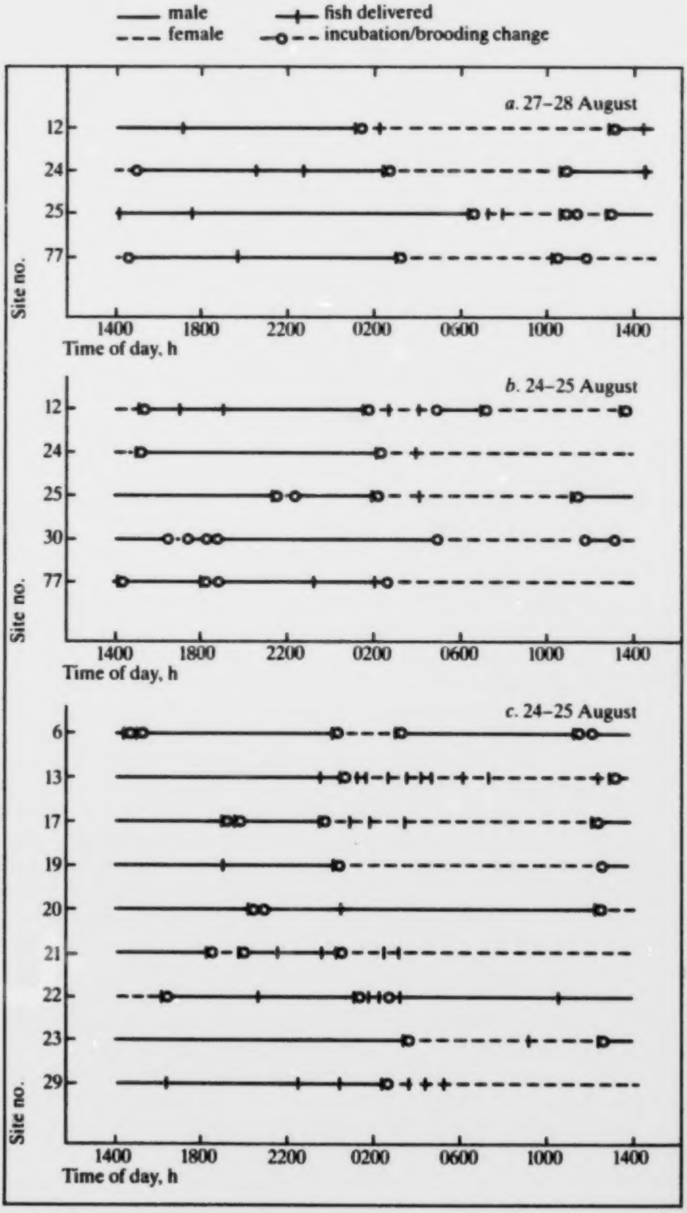
* Values in parentheses are percentages.

their time to feeding to satisfy the additional energy demand imposed by producing an egg. The number of males present exceeded the number of females on 8 of 9 days ($P = 0.02$, binomial test). Following the re-laying of all five eggs, however, females were present on 75% of site-days and exceeded the number of males present on all but 1 day between 22 July and 8 August (Table 10).

In all incubation changes observed between pairs of known sex during 1400–1800 h, the male relieved the female ($N = 21$, $P < 0.001$, binomial test). If this sample is representative of the whole population it suggests that by this stage in the season females normally incubate during the early part of the day, males taking over during the afternoon. In fact, the majority of exchanges between the members of the sexed pairs took place between 1700 and 1800 h and the synchronized arrival of males would therefore explain the peak of incubation changes recorded at 1800 h. The other peak at 0600 h may indicate the reverse situation, with females relieving males at the majority of sites. The incubation schedule of the sexed pairs, all having relaid eggs, is probably not typical of the early part of the incubation period when the low rate of exchanges excludes the possibility of 12-h shifts.

Vocalizations during the incubation and chick-rearing periods include a deep, gutteral laughing noise described by Pennycuick (1956) as "haw-haw-haw. . ." Tuck (1961) described how this call spreads slowly through the colony, particularly at night, being passed on from one bird to the next. The bird stands up and points the bill downwards towards the egg or chick as it delivers the call. Thus this call may train the chick to recognize its parent's voice. The chain reaction can then be explained by the need for each bird to remind its chick of its own call following the vocalization of neighbouring birds. The fact that it occurs more frequently at night (supported by casual observations in the present study) suggests that it is given mainly by the male. This is logical since it is the male which accompanies the chick at fledging, when vocal recognition is most important (see this chapter, section 4.8).

**Figure 29**
**Incubation (site 30) and brooding of chicks (all other sites) by the male and female parents during two 24-h watches at plot U in 1977: (*a*) and (*b*) pairs containing one colour-marked bird of known sex (all cases involve relaid eggs) and (*c*) pairs of unknown sex (sexes are inferred from timing of change-overs.)**



### 4.3. Chick-rearing period

Two continuous 24-h watches made on 24 and 27 August at plot U showed that both parents brooded fairly solidly for 12 h each; females arrived and exchanged mainly at 2300–0300 h and males at 1200–1500 h (Fig. 29). Exchanges at other times tended to be followed soon afterwards by another exchange, so that between 1500 and 2300 h the majority of birds present were males, whereas between 0300 and 1200 h the majority were females.

P.G.H. Evans and party (pers. commun.), watching from Horse Head Island, 24 km to the south of the large Thick-billed Murre colony at Agparssuit, West Greenland, and almost on the same latitude as Prince Leopold Island, made round-the-clock counts of murres passing north and south through the channel to the east of the island during the late incubation and early chick-rearing periods. They noted two peaks of movement for birds flying towards the colony, at 0200 and 1200 h, presumably corresponding to the arrivals of females and males respectively. The pattern of outbound birds was rather different, with a small peak at 0200 h, perhaps corresponding to the departure of males, and a much larger peak at 1800 h. The second peak may represent the exodus of the majority of prospecting birds.

Assuming that females brood mainly in the morning, we can compare the relative numbers of fish brought by the two parents. No difference in feeding rate was found between the sexes either on 24 or 27 August, males bringing fish more frequently than females at 9 sites and females bringing more than males at 11 sites (Table 11).

On average, about half of the birds arriving with fish exchanged with the brooding bird, but this was partly dependent on the feeding rate. On 19 August 1977, with the feeding rate only a third of the average for that year due to a blizzard, 89% of feeding visits were followed by an exchange. Birds brought up to four food items in a run, or exceptionally as many as 10 (Table 12), although in the latter case the items were very small and the intervals between food deliveries were brief.

If the bird arriving with food exchanged with the brooding bird, both birds generally spent more time at the site than if no exchange occurred. The difference, however, was not great. The time spent at the site by both parents was inversely related to the age of the chick, particularly up to the age of about 10 days (Fig. 30) and this correlation accounts for an apparent decline with date (Fig. 31).

After the age of 10 days the parents are unable to feed their chick rapidly enough to allow it to maintain its maximum potential rate of weight increase (Chapter IV, section 3) and hence, presumably, the amount of time that the parents can afford to spend at the site reaches a lower limit at this point. This would also explain why the mean durations for given dates in 1976 and 1977 were similar, despite differences in feeding rates. Some indication of a seasonal trend is also apparent when chicks less or more than 10 days of age are compared separately (Table 13), and this may reflect the pressure on the parents of late-hatched chicks to accelerate their development as far as possible.

Birds leaving their site after an exchange usually exhibited the "butterfly flight" and flew steeply down to land on the sea within 500 m of the colony. When no exchange occurred, however, the "but-

**Table 11**
The numbers of fish delivered to chicks at plot U by male and female parents on 24 and 27 August 1977

| | 24 August | | 27 August | |
|---|---|---|---|---|
| Site no. | Male | Female | Male | Female |
| Marked pairs* | | | | |
| 12 | 4 | 4 | 2 | 2 |
| 24 | 2 | 1 | 1 | 3 |
| 25 | 2 | 2 | 4 | 3 |
| 77 | 1 | 3 | 1 | 2 |
| Subtotals | 9 | 10 | 8 | 10 |
| Unmarked pairs | | | | |
| 6 | 2 | 3 | 3 | 4 |
| 13 | 10 | 2 | 3 | 4 |
| 17 | 4 | 2 | — | — |
| 19 | 1 | 2 | — | — |
| 20 | 0 | 4 | — | — |
| 21 | 3 | 4 | 3 | 3 |
| 22 | 4 | 3 | 3 | 2 |
| 23 | 2 | 1 | 2 | 2 |
| 29 | 3 | 4 | 1 | 2 |
| 55 | — | — | 5 | 3 |
| 78 | — | — | 4 | 3 |
| Subtotals | 29 | 25 | 24 | 23 |
| Totals | 38 | 35 | 32 | 33 |

* Marked pairs for which the sex of both birds was known.

**Table 12**
Numbers of fish brought by individual birds between incubation exchanges at plot U on 24 and 27 August 1977

| | No. of fish | | | | | | | | | | Median no. of |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | deliveries/bird |
| 24 August | 23 | 8 | 4 | 5 | — | — | — | — | — | 1 | 1.56 |
| 27 August | 10 | 7 | 8 | 2 | — | — | — | — | — | — | 1.37 |

**Table 13**
Time spent between arrival and exchange of brooding duty after chicks had been fed, in relation to date and the age of the chicks in 1976 and 1977

| | Mean duration, min | | Mann-Whitney | |
|---|---|---|---|---|
| Date | Chick < 10 days old | Chick > 10 days old | *U* | *P* (2-tailed) |
| 31 July 1976 | 20.67 (9)* | — | — | — |
| 7 August 1977 | 16.70 (20) | 2.60 (5) | 7 | 0.002 |
| 12 August 1977 | 6.69 (13) | 2.73 (15) | 137 | 0.068 |
| 18 August 1977 | 5.33 (6) | 1.94 (35) | 63 | 0.120 |

* Values in parentheses are sample sizes.

**Figure 30**
Time elapsing between arrival and exchange of brooding duty in relation to age of chicks during three watches at plot S1 in 1977

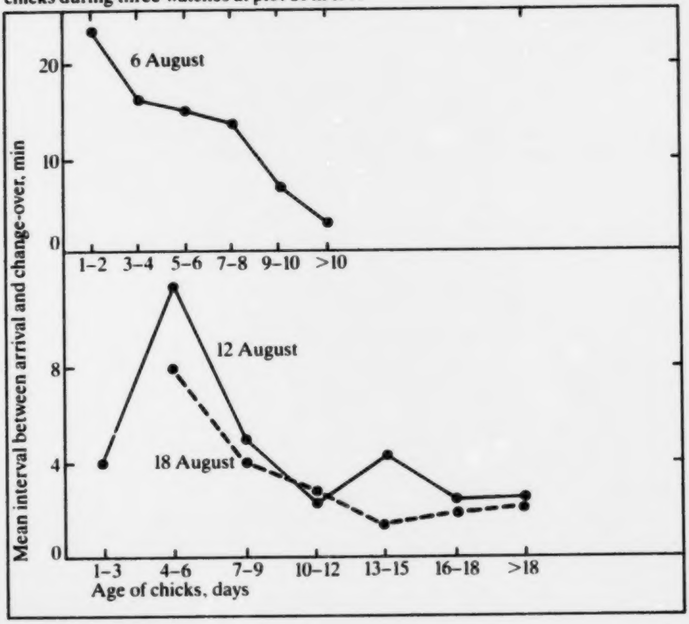
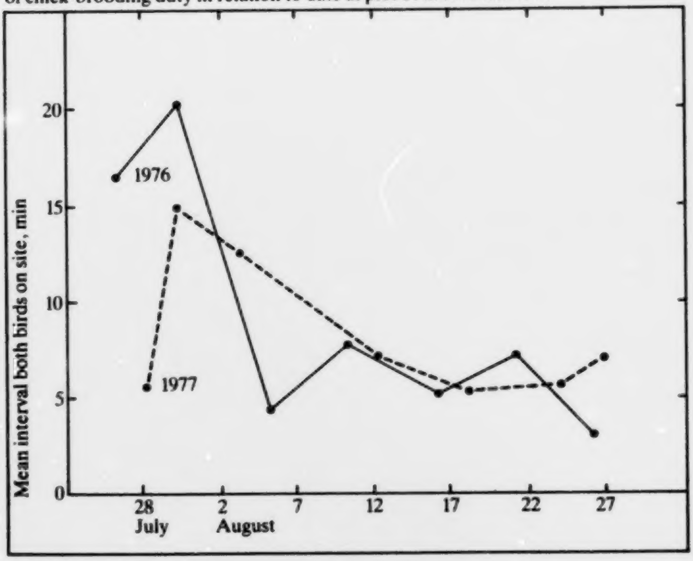


**Figure 31**
Mean duration of time spent by both members of a pair at the site during exchanges of chick-brooding duty in relation to date at plot S1 in 1976 and 1977



terfly flight" was less common and departing birds usually flew steadily away from the colony until lost from sight, presumably heading for their feeding area (Table 14). Those birds did not necessarily form into flocks while within sight of the island, whereas virtually all birds leaving from the sea did.

Both Birkhead (1976*a*), working on Common Murres, and Ashcroft (1976), working on Atlantic Puffins *Fratercula arctica*, observed that departures from small areas of the colony tend to be more synchronized than would be predicted by a random model. Ashcroft also found arrivals to be significantly synchronized and both authors discuss their findings in relation to the "information centre" theory (proposed by Ward and Zahavi 1973), which predicts clumping of departures where birds are taking cues from one another on the location of feeding areas.

At Prince Leopold Island the departures of site-holders were not found to be significantly synchronized, although this is not surprising since most birds flew down to the water rather than flying directly to the feeding area. Arrivals during the chick-rearing period at plot S1 approximated very closely a random distribution, suggesting that if birds from the same part of the cliff were using the same feeding area, then they showed no tendency to synchronize their return to the colony. This conclusion was supported by observation of flocks heading towards the colony during the chick-rearing period. Those flocks generally broke up when they came within ca. 0.5 km of the cliffs, and individual birds scattered over a wide area of the colony. The lack of synchrony in arrivals and departures from and to the cliffs does not offer evidence for rejecting the information centre concept, but it does suggest that if information is transferred the exchange does not take place on the cliffs. The idea is discussed more fully in Chapter V, section 4.7.

**Table 14**
Behaviour of birds leaving their site after their chick had been fed, in relation to whether or not there had been an incubation exchange

| Behaviour | Exchange | No exchange | chi$^{2}$* | *P* |
|---|---|---|---|---|
| a. "Butterfly flight" | 15 | 2 | 4.62 | < 0.05 |
| b. No "butterfly flight" | 7 | 8 | | |
| a. Landed on the sea | 17 | 0 | 13.53 | < 0.01 |
| b. Flew until out of sight | 5 | 10 | | |

* Incorporates Yates correction for continuity.

## 4.4. Behaviour of prospectors

A variety of observations suggested that the proportion of prospecting birds visiting the colony increased during the summer. The rate of arrival of prospectors at plot S1 increased in both 1975 and 1977 from means of about 10 arrivals/h in early July to more than 50 arrivals/h in August, with peaks of more than 130 arrivals/h in 1977 (Fig. 32). In 1975 we counted the ledges at plot G1 separately during the daily counts. At ledges where no eggs were laid, and where therefore all birds were probably non-breeders, numbers increased gradually until 14 July, but accelerated sharply thereafter to a peak in mid August (Fig. 33).

Changes in the rates of arrival and the lengths of time spent by prospecting birds on the cliffs could be accounted for either by changes in the behaviour of individual birds, or by changes in the composition of the prospecting segment of the population during the season. Casual observations of behaviour suggest that in all 3 years a major influx of new prospectors occurred between 15 and 20 July. At this time large flocks of murres appeared, flying back and forth parallel to the cliffs. This behaviour was similar to that recorded just after the arrival of the first murres in May, except that the flocks seen in July usually flew very high, at or above the level of the cliff-top. At first these flocks did not attempt to land on the cliffs, but circled out to sea when they reached the end of the colony. Their behaviour suggests that they were visiting the colony for the first time, at least in that year.

The behaviour of at least some of the birds taking off from the cliffs also changed in the second half of July. During June most birds seen taking off from the cliffs either flew down to land on the sea, or returned to land within a few metres of the point from which they had originally departed. After about 15 July, however, a large proportion

**Figure 32**
Rates of arrival of prospecting birds during 24-h watches in 1975 and 4-h watches in 1977 at plot S1

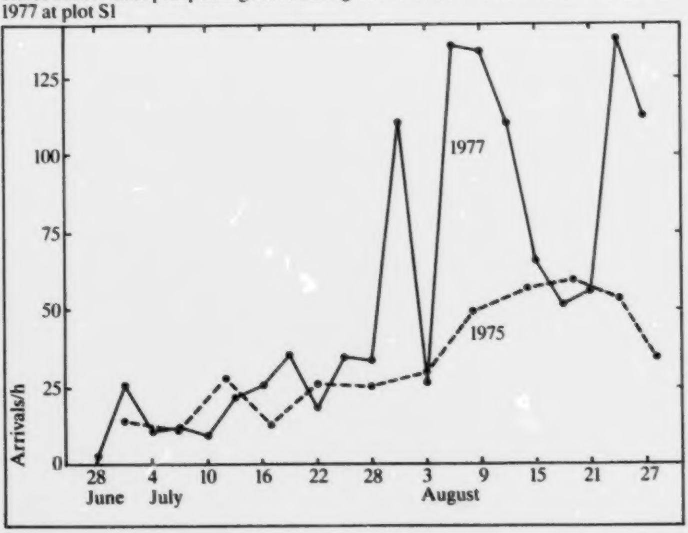


**Figure 33**
Numbers of birds counted on ledges not used for breeding as percentage of total count at plot G1 in relation to date, and changes in the total count of birds, expressed as 7-day means for 1975

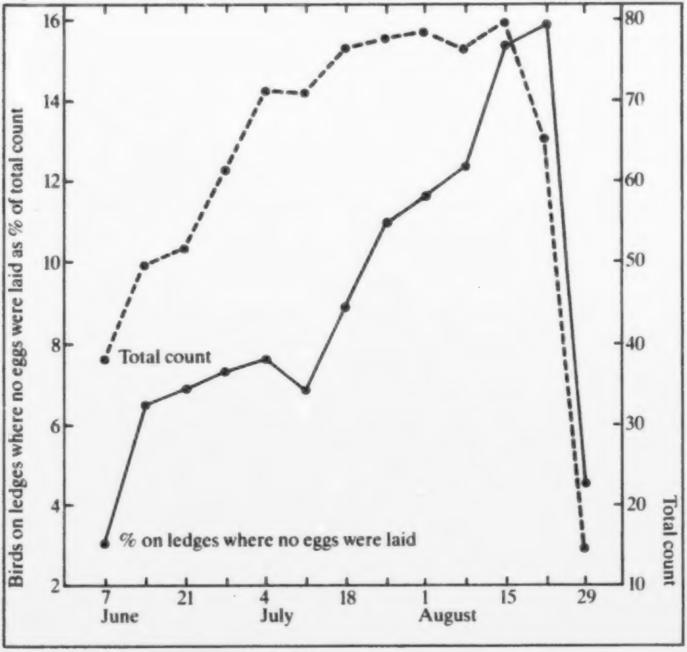


**Figure 34**
Proportion of birds observed leaving the cliffs and returning to land more than 20 m from their original point of departure, in relation to date. All observations in 1977 except for single date in 1975 ( + )

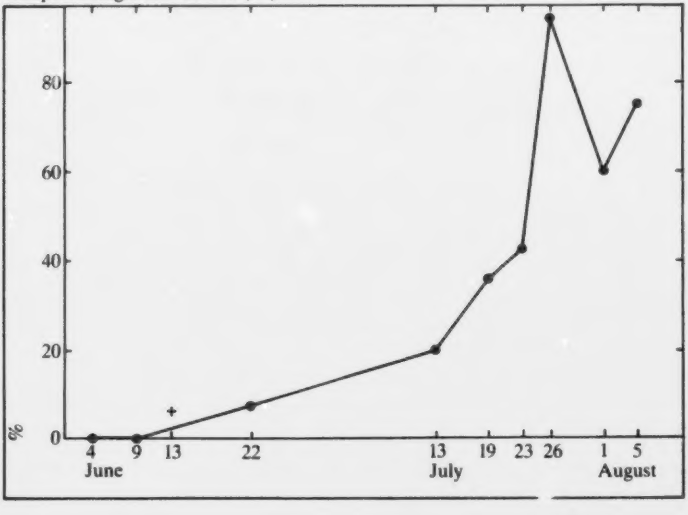
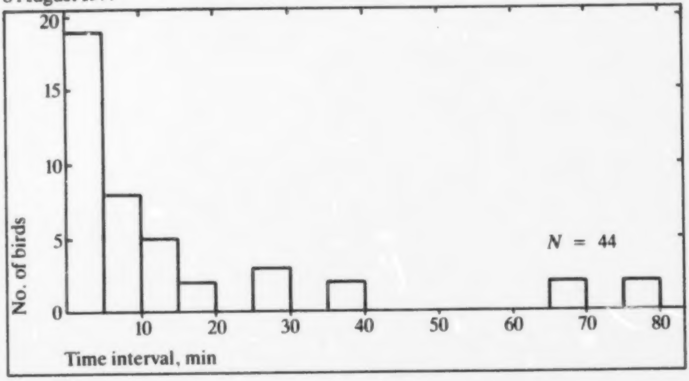


**Figure 35**
Duration of time spent on plot S1 by individual prospectors, 23–29 July and 8 August 1977



of birds seen leaving the colony circled out to sea and then returned to land some distance from their point of departure, suggesting that these individuals had no attachment to a particular site (Fig. 34). Some examples of the trajectories of birds taking off from the cliffs on 26 July 1977 are quoted below (AJG):

(1) Circles out to sea, returns and flies close to the cliff 200 m from point of departure, circles again and "buzzes" spot 100 m from point of departure, circles out to sea, then returns to land 150 m from departure point, wings flapping, falls off after 15 s.
(2) Circles out to sea, returns and lands about 40 m from point of departure, wings flapping. Is pecked almost immediately by another bird and falls off.
(3) Circles, returns to touch the cliff 30 m from point of departure, but pushes off immediately, circles out to sea, returns, touches again 60 m from point of departure, circles, then lands 10 m from point of departure.

It was difficult to follow individual birds for long among the throng of murres around the cliffs, but some prospecting birds clearly spent a large proportion of their time in the vicinity of the colony in flight at this stage of the season.

The time spent by prospecting birds on the cliffs, recorded during several watches at plot S1, ranged from a few seconds to more than 1 h (Fig. 35). Most birds landed on broad, sparsely occupied ledges, usually near the seaward edge (Fig. 36). On arrival, birds frequently walked around the plot, occasionally sitting down briefly and interacting with site-holders and with other prospectors. Figure 37 illustrates representative explorations.

When pecked at by site-holders, prospecting birds generally retreated without retaliating and consequently we did not record these interactions as fights. Nevertheless site-holders were commonly aggressive towards prospectors and 25% ($N = 57$) of prospectors watched at S1 departed following aggressive interactions with site-holders.

The rate of arrival of prospecting birds varied with time of day in a similar way to the variation in counts. During the incubation period (July) arrivals were most frequent at 0600 h, with a smaller, perhaps insignificant peak at 1400 h. In the chick-rearing period the relative size of the two peaks was reversed, with the main peak falling between 1200 and 1600 h (Fig. 38).

In the second half of August, in all 3 years, we saw a small number of murres in winter plumage on the water at the foot of the cliffs, but never recorded birds in this plumage on the cliffs. These were probably birds in their first year which had failed to undergo a spring body moult. If so, young birds apparently continue to arrive in the vicinity of the colony up to the end of the season, although because these latecomers do not visit the cliffs they would have no effect on attendance patterns.

**Figure 36**
Sketch of plot S1 showing the places where prospecting birds landed during watches in July 1977 (drawn from study plot photo, App. 1)

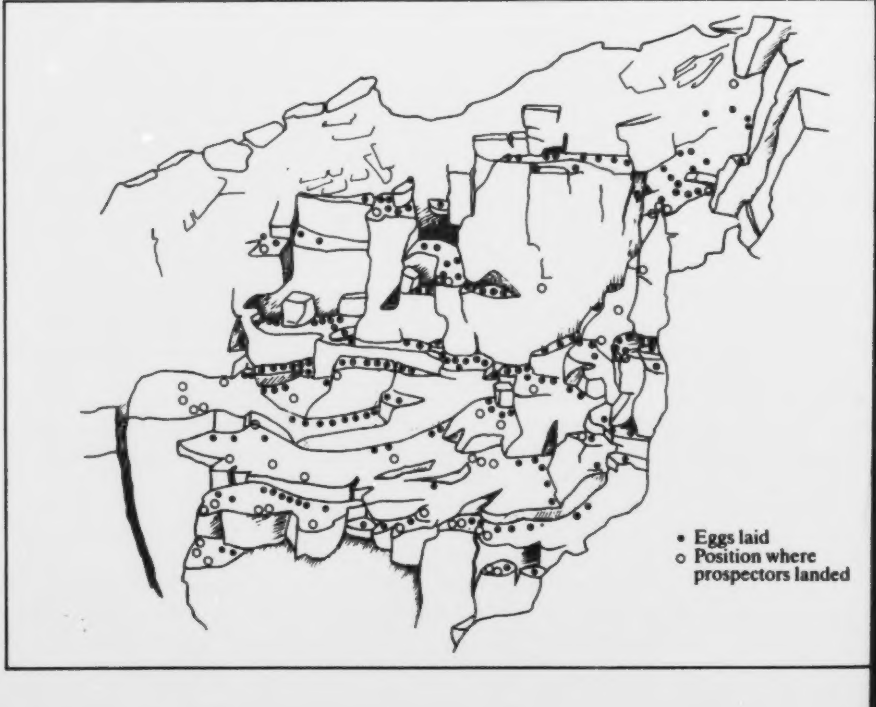


**Figure 37**
Sketch of plot S1 showing the routes walked by four prospecting birds watched in July 1977 (drawn from study plot photo, App. 1)

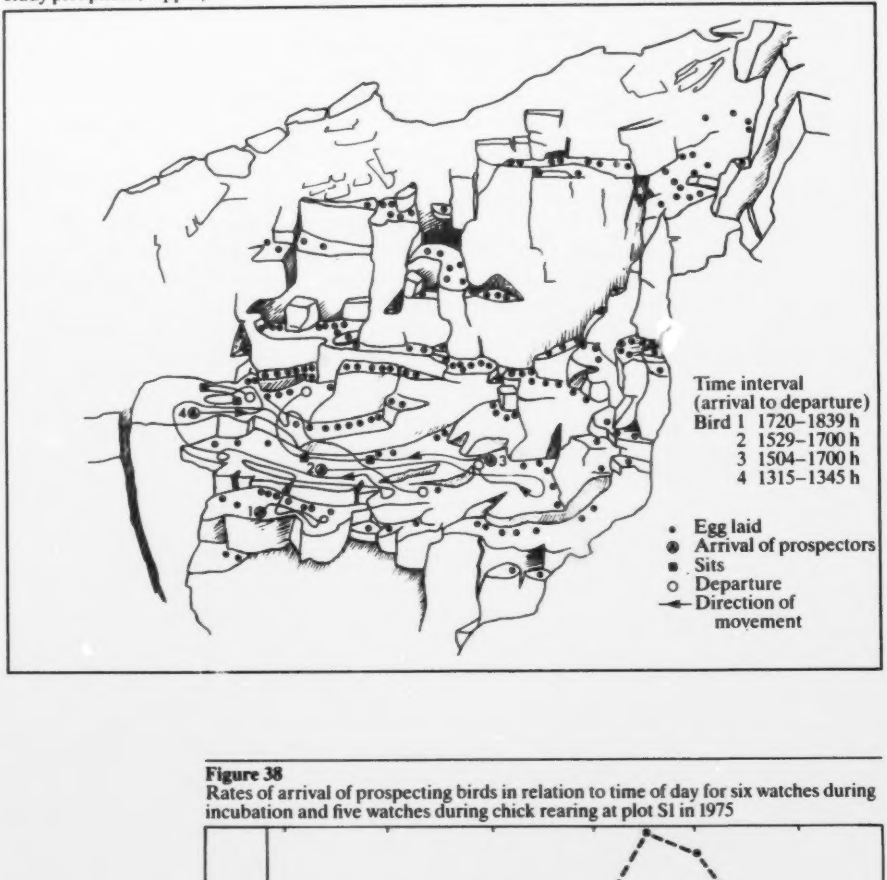
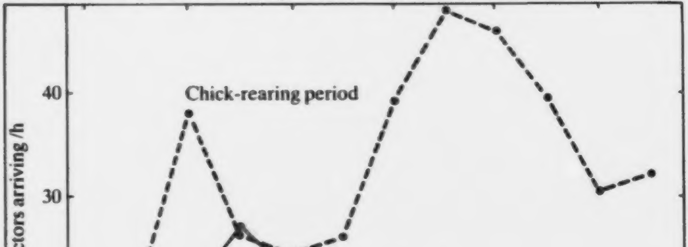

4
2
3
1
Time interval
(arrival to departure)
Bird 1 1720–1839 h
2 1529–1700 h
3 1504–1700 h
4 1315–1345 h
• Egg laid
● Arrival of prospectors
■ Sits
○ Departure
← Direction of movement

**Figure 38**
Rates of arrival of prospecting birds in relation to time of day for six watches during incubation and five watches during chick rearing at plot S1 in 1975



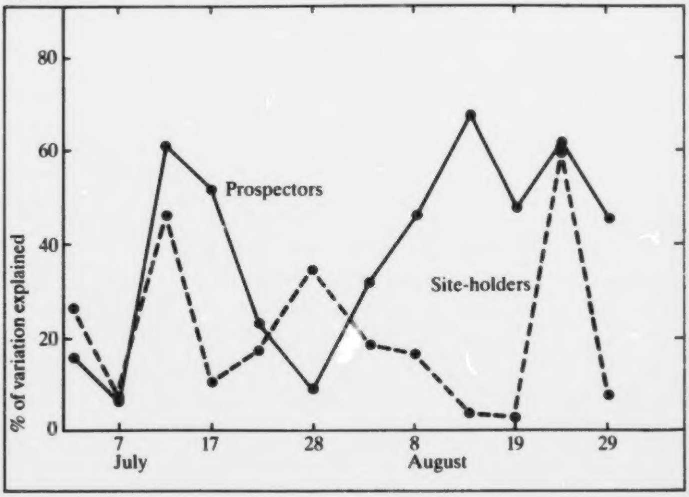
## 4.5. Role of prospectors in determining fluctuations in attendance

The similarity between seasonal and daily fluctuations in the rate of arrival of prospecting birds and fluctuations in the numbers of birds counted suggests that the activity of prospectors may be a major factor determining observed patterns of attendance at the colony. The inter-plot variation in the size of seasonal fluctuations noted in section 3.2 of this chapter also supports this hypothesis. Unfortunately, we could not identify the status of birds present during a brief count, and we therefore need to understand the role of prospectors in determining overall attendance patterns in order to use data from counts to monitor changes in population levels.

Data from 24-h watches in 1975 revealed a significant correlation between the number of prospectors arriving during a 1-h period and the count at the end of the period. The proportion of the daily variation in counts explained by the rate of arrival of prospectors was high on 12 and 17 July and again from 8 August onwards, and exceeded the proportion explained by the arrival of site-holders on 9 out of 12 watches (Fig. 39). A strong correlation was found, however, between the rate of arrival of prospectors and the rate of incubation changes (Fig. 40), and hence the effects of prospectors and site-holders are likely to be additive.

Counts made during 4-h watches at S1 in 1977 showed that the numbers present were positively correlated with the rate of arrival of prospectors ($r = 0.546$, $N = 22$, $P < 0.01$) and this correlation was considerably improved if the first watch (28 June) and the last two (27 and 30 August) were omitted ($r = 0.758$, $N = 19$, $P < 0.01$). A $\log_{10}$ transformation improved this correlation still further, explaining 61% of the variation in counts between 31 June and 24 August inclusive

**Figure 39**
The proportion of variation in counts made every 2 h at plot S1 explained by the correlation between numbers and the rate of arrival of prospectors and site-holders for 1975



(Fig. 41). Counts were also positively correlated with the number of site-holders arriving ($r = 0.646$, $N = 19$, $P < 0.01$), but a step-up multiple regression analysis showed that the rate of arrival of site-holders did not add significantly to the amount of variation explained by the arrival of prospectors alone.

Rates of arrival of prospectors were analysed in relation to weather conditions recorded during the watch for the period from 25 July onwards. A significant negative correlation was found with wind speed ($r = -0.700$, $N = 14$, $P < 0.01$) and a positive correlation with visibility ($r = 0.710$, $N = 14$, $P < 0.01$). A step-up multiple regression analysis showed that both contributed significantly, together accounting for 64% of the variation in the rate of arrival.

The effect of the rate of arrivals on the number of birds present must be dependent on the length of time spent on the plot by individual birds following their arrival. Unfortunately, the length of visits was difficult to determine because, without marked birds, individuals had to be kept under constant observation and the chance of losing

**Figure 40**
Relationship between the frequency of incubation changes and the number of prospectors arriving during 4-h watches at plot S1 in 1977

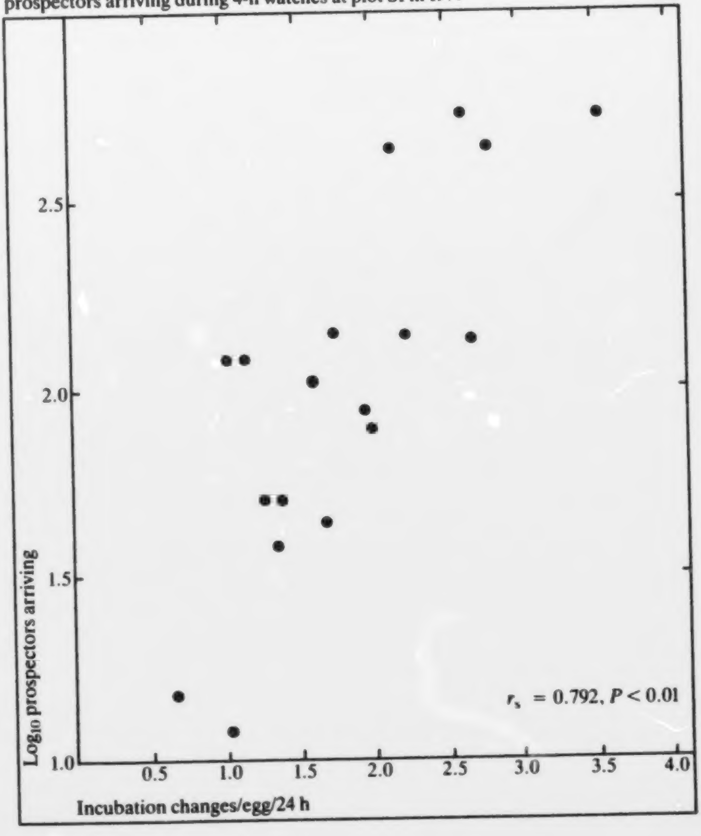
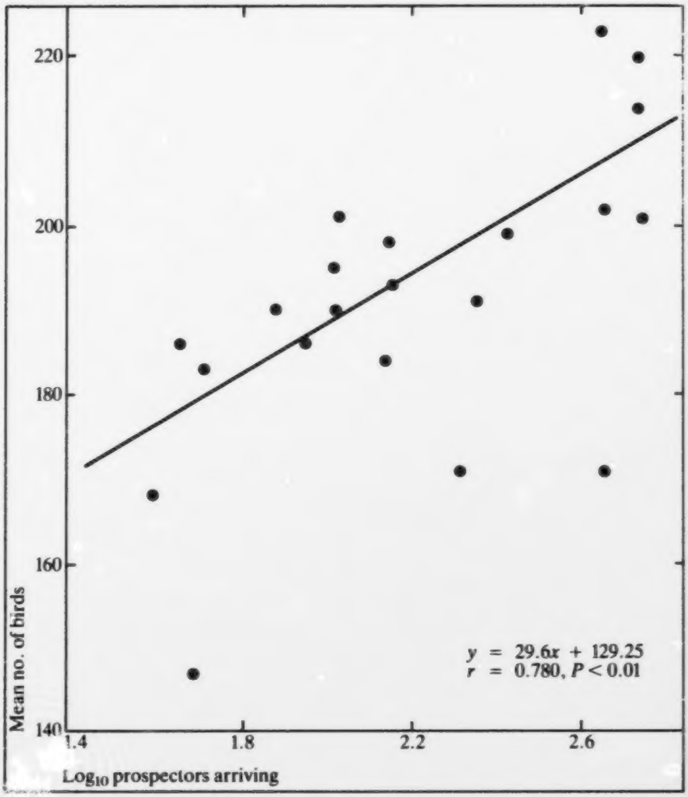


**Figure 41**
Relationship between the total number of birds present and the number of prospectors arriving during 4-h watches at plot S1 in 1977. Solid line shows the regression of numbers on rate of arrival



track of them increased with the length of time that they stayed. The non-linear relationship between rates of arrival and counts, however, suggests that visits during periods when rates of arrival were high must have been shorter than when rates were low.

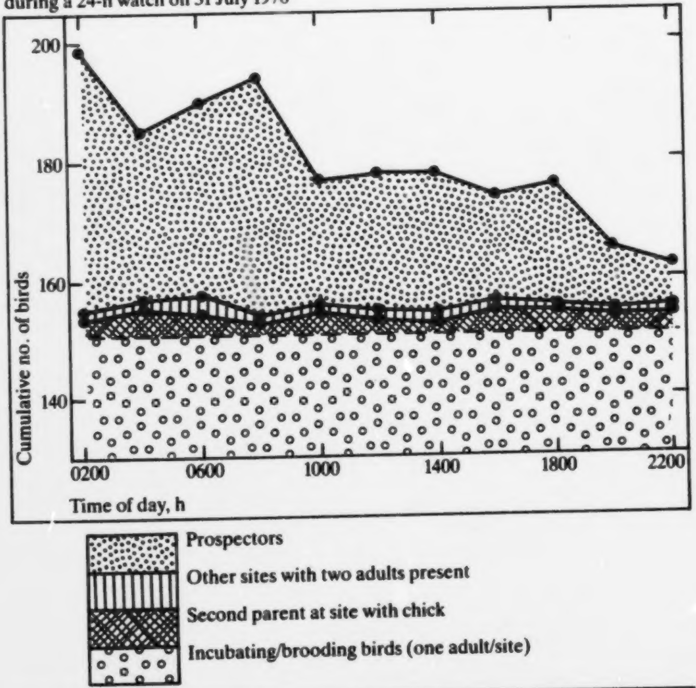
We recorded the lengths of visits by site-holders throughout the day on 31 July 1976, which allowed us to calculate the mean number of sites at which both members of the pair were present. The contribution of prospectors to changes in the total numbers of birds present is clearly illustrated when the contribution of site-holders is known (Fig. 42) and may have been particularly marked on 31 July because increasing wind speed and decreasing visibility during the watch apparently caused a steep decline in the rate of arrivals. The amount of variation in counts explained by the rate of arrival of prospectors was 69%, higher than for any watch during 1975.

On 21 August 1976, when we made similar observations, the attendance of birds at failed sites or at those where the chick had fledged, and not the rate of arrival of prospectors, determined the variation in counts. The proportion of these sites occupied was recorded every 2 h and numbers fell sharply after 1600 h, at a time when the arrival rate of prospectors was increasing (Fig. 43). Differences in the pattern of attendance of site-holders and prospectors after the majority of chicks have fledged may account for the fact that counts on 27 and 30 August 1977 were below the level predicted by the regression of counts on arrivals for the rest of the season.

The relatively small amount of daily variation in counts explained by the arrival of prospectors during watches on 22 and 28 July and 3 August 1975 (Fig. 39) may be connected with the influx of näive birds in mid July as postulated above (see this chapter, section 4.4). Immediately after arriving at the colony these birds might be expected to make only brief landings on the cliffs and hence high rates of arrivals during this period may not necessarily be correlated with high counts.

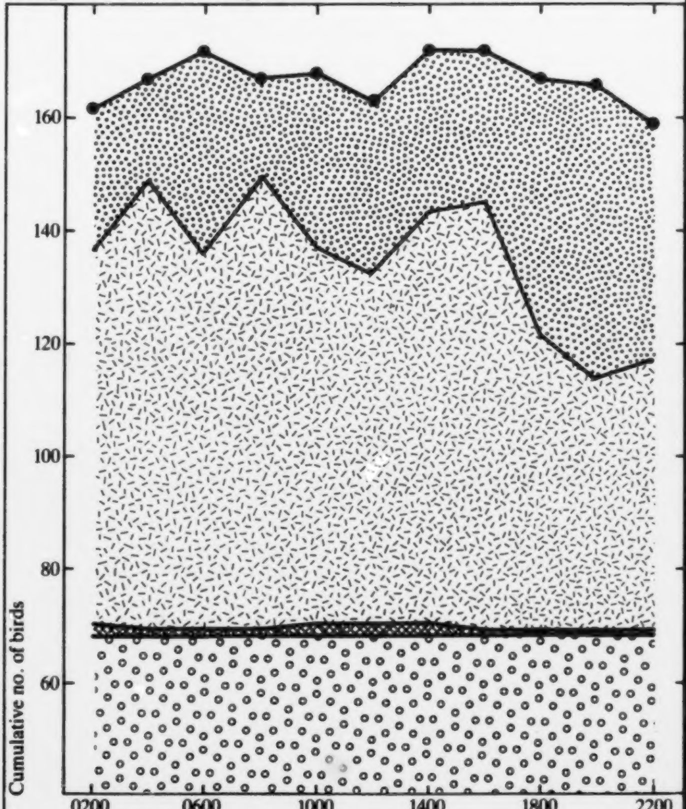
Thus, from mid July to mid August the rate of arrival of prospecting birds apparently is the most important factor influencing patterns of attendance at the colony. Changes in rates of arrival of prospectors over 24 h parallel those of site-holders and both groups of birds may be synchronizing their behaviour to a common factor, such as a daily fluctuation in the abundance of food. It seems more likely, however, that prospectors simply model their behaviour on that of the site-holders.

**Figure 42**
Contribution of different categories of birds to total numbers present on plot S1 during a 24-h watch on 31 July 1976



Birkhead and Hudson (1977) have used maximum counts of non-breeding birds to estimate the proportion of non-breeders in the population of Common Murres on Skomer Island, Wales. Non-breeding Common Murres collect in "clubs" on rocks at the base of the cliffs, where they can readily be counted. Unfortunately, we did not observe such congregations at Prince Leopold Island and club behaviour, if it exists, probably occurs on the sea just off the colony. Birds on the water often occur in groups or lines of up to 100 individuals and these aggregations occasionally take off together and fly

**Figure 43**
Contribution of different categories of birds to total numbers present on plot S1 during a 24-h watch on 21 August 1976



back and forth along the cliffs, suggesting that the birds are prospectors. Large numbers of breeding birds, however, also occur on the sea at the base of cliffs, because birds relieved from incubation or brooding duties often fly directly to the water. Hence counts of birds on the water include all birds, not only non-breeders.

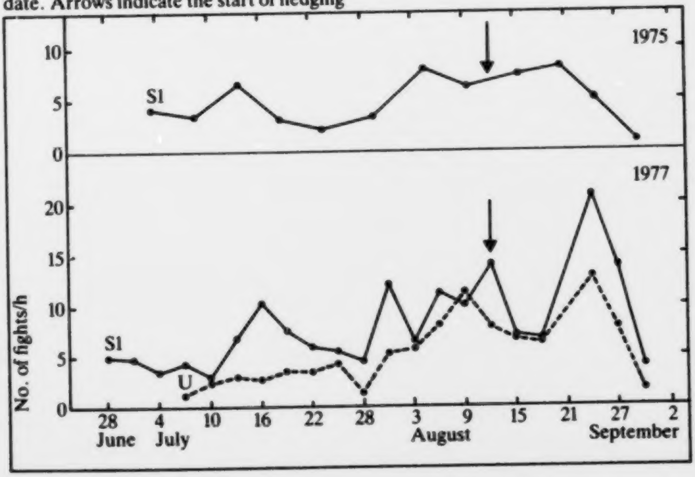
The number of non-breeders can be estimated, however, from maximum daily counts, using estimates of the number of breeders present based on the length of time spent by both members of a pair on the site. Estimating the breeding population of count plots as 850 pairs (828 eggs were laid in 1976) and assuming that both members of the pair are present for an average of 1 h in 24, the total number of breeders present should not exceed 900 birds. Peak numbers during daily counts were 1150 in 1976 and 1310 in 1977, giving estimates for the number of non-breeders present of 250 and 410 or 13 and 19% respectively, of the total population (excluding at least some first-year birds). These are minimum estimates as it seems unlikely that all non-breeders would ever be present on the cliffs simultaneously. These estimates, however, are similar to the 15% estimated for the Skomer Island population by Birkhead and Hudson (1977).

## 4.6. Aggression during incubation and chick rearing

The frequency of fighting was generally lowest during incubation, rising sharply in late July (early chick-rearing period) 1975 and 1977 to a peak in the second half of August, after the start of fledging (Fig. 44). The apparently lower incidence of fighting in 1975 compared with 1977 is due to the fact that 1975 figures are derived from watches on alternate hours over 24 h, rather than the 1400–1800 h periods used in 1977, which was the daily peak of arrivals during chick rearing.

As in the pre-laying period, the number of fights was related to the rate of arrivals at the plot: in 1977 we recorded both the highest number of fights and the maximum rate of arrival of prospecting birds

**Figure 44**
Frequency of fights on plot S1 in 1975 and 1977 and on plot U in 1977 in relation to date. Arrows indicate the start of fledging

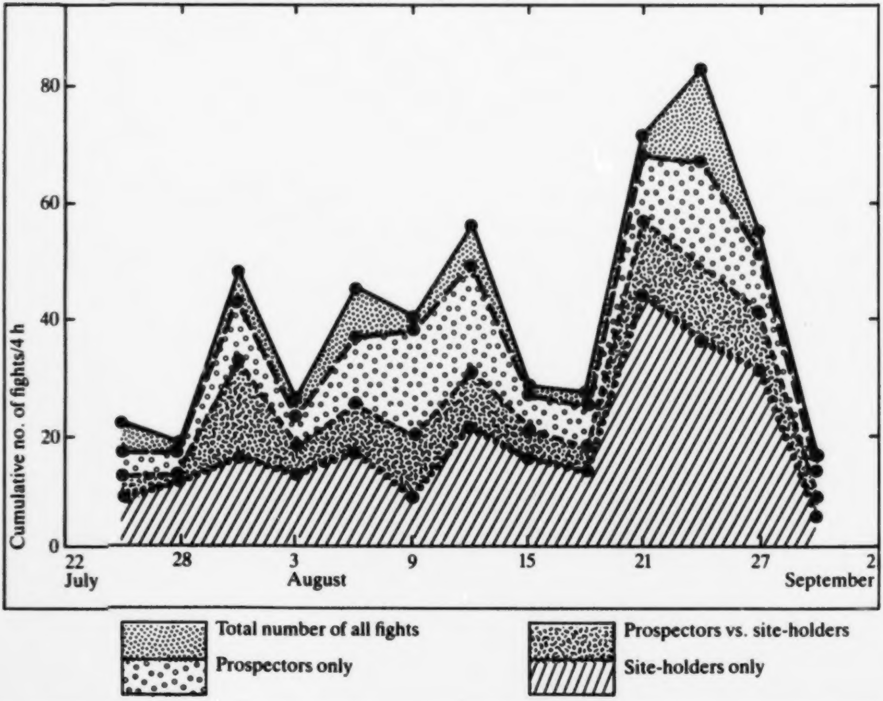


on 24 August. Data from the 24-h watches in 1975 showed that the rate of arrival of prospectors explained 65% of the seasonal variation in the incidence of fights ($r = 0.808$, $N = 11$, $P < 0.01$). In 1977 the rate of arrival of prospectors explained 61% of the variation among regular 4-h watches ($r = 0.780$, $N = 13$, $P < 0.01$; using the period from the start of hatching, 25 July onwards) compared with only 36% explained by arrivals of site-holding birds ($r = 0.601$, $N = 13$, $P = 0.025$).

Despite the correlation between the number of prospectors arriving and the number of fights, prospectors were involved in only 43% ($N = 535$) of all fights during the period from 25 July onwards in 1977, compared with 46% in which both participants were site-holders (status of one of the birds was unknown in 11% of cases). The peak of fighting in the second half of August appears to be largely the result of an increase in the number of fights between site-holders (Fig. 45).

The frequency of fighting during the chick-rearing period was related to the date of hatching and the number of neighbours adjacent to the site (see Chapter III, section 4 for definition). Between 25 July and 18 August 1977, a mean of 0.28 ($N = 16$) fights per 4-h watch occurred at sites where chicks hatched before 31 July, compared with 0.18 ($N = 23$) at sites where chicks hatched after 9 August (Table 15). During the same period sites with no neighbours averaged 0.11

**Figure 45**
Fights observed at plot S1 in 1977 in relation to the status of birds involved. Categories are summed cumulatively with the total number of fights, including some fights between birds of unknown status



($N = 36$) fights per watch, compared to 0.30 ($N = 48$) at sites with two or three neighbours (Table 16). Of the sites observed for behaviour, eggs on sites with no neighbours hatched slightly earlier than those on other sites, and hence the effects of date of hatching and number of neighbours appear to be independent. Birkhead (1978*a*) recorded a similar correlation between breeding pair density and the incidence of aggressive behaviour for the Common Murre.

When we analysed single watches, birds with chicks were involved in more fights than were birds with eggs (Table 17), but in fewer fights than birds with no egg or chick (Table 18). The same effect was

**Table 15**
Frequency of fighting at sites where chicks hatched in relation to the date of hatching at plot S1 between 25 July and 18 August 1977

| | Total fights recorded | | | | | | | Mean number/site/watch |
|---|---|---|---|---|---|---|---|---|
| Date of hatch | 0 | 1 | 2 | 3 | 4 | 5 | ≥6 | ($N = 9$) |
| Before 31 July | 5 | 0 | 4 | 1 | 2 | 3 | 1 | 0.28 |
| 31 July – 3 August | 5 | 8 | 6 | 6 | 7 | 1 | 2 | 0.26 |
| 4–8 August | 7 | 9 | 3 | 3 | 6 | 2 | 0 | 0.21 |
| After 9 August | 5 | 9 | 5 | 1 | 0 | 3 | 0 | 0.18 |
| Totals | 22 | 26 | 18 | 11 | 15 | 9 | 3 | 0.23 |

Median test for correlation: $\text{chi}^2 = 4.61$, $P < 0.05$.

**Table 16**
Frequency of fighting at sites in relation to the number of neighbours at plot S1 between 25 July and 18 August 1977.

| No. of | Total fights recorded* | | | | | | | | Mean no./site/watch |
|---|---|---|---|---|---|---|---|---|---|
| neighbours | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | ($N = 9$) |
| 0 | 13 | 13 | 8 | 1 | 1 | 0 | 0 | 0 | 0.11 |
| 1 | 12 | 14 | 10 | 6 | 10 | 7 | 1 | 1 | 0.25 |
| 2 or 3 | 3 | 15 | 7 | 8 | 8 | 2 | 3 | 2 | 0.30 |
| Totals | 28 | 42 | 25 | 15 | 19 | 9 | 4 | 3 | 0.23 |

* Testing sites with 0 or 1 fight against those with more (median): $\text{chi}^2 = 11.37$, df 2, $P \leq 0.01$.

**Table 17**
Incidence of fighting at sites in relation to the presence of eggs or chicks at plot S1 in 1977

| | Mean no. of fights per site* | | |
|---|---|---|---|
| Date | Sites with eggs | Sites with chicks | Sites where no egg was laid |
| 31 July | 0.27 (92) | 0.45 (29) | 0.09 (11) |
| 3 August | 0.15 (68) | 0.26 (53) | 0.09 (11) |
| 6 August | 0.12 (42) | 0.37 (79) | 0.36 (11) |
| 9 August | 0.10 (29) | 0.20 (92) | 0.27 (11) |

* Values in parentheses are sample sizes.

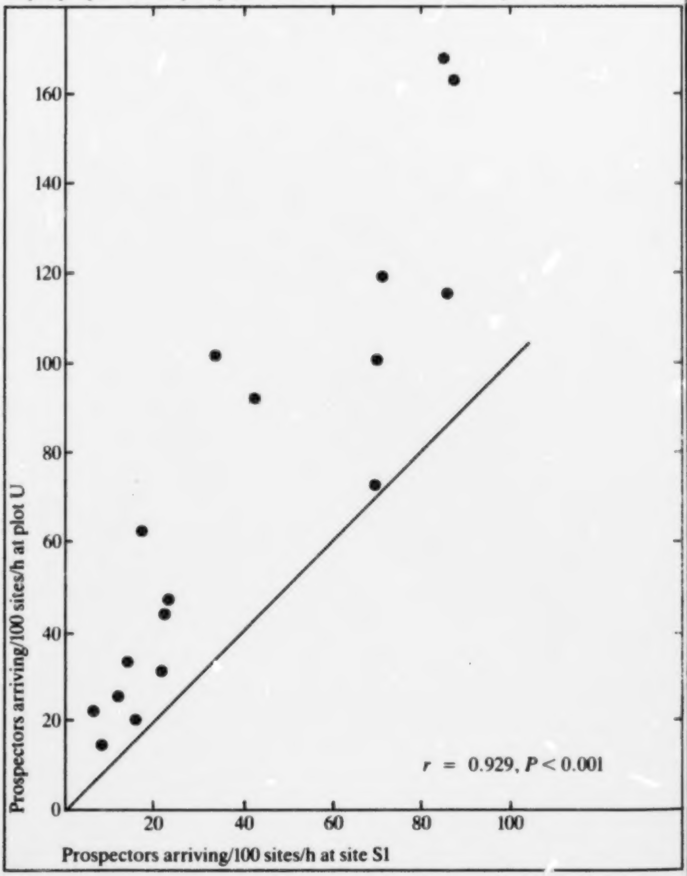
**Table 18**
Incidence of fighting at sites in relation to whether a chick was present, had fledged, or disappeared prematurely, at plot S1 in 1977

| | Mean no. of fights per site* | | |
|---|---|---|---|
| Date | Sites with chicks | Sites where chicks had fledged or disappeared | Sites where no egg was laid |
| 18 August | 0.17 (104) | 0.50 (14) | 0 |
| 21 August | 0.67 (91) | 0.81 (27) | 0.73 |
| 24 August | 0.44 (45) | 0.68 (73) | 0.27 |

* Values in parentheses are sample sizes.

found for individual sites; fighting increased at 46 sites between the two watches prior to and the two watches following hatching, while it decreased at 12 sites ($P \leqslant 0.001$, binomial test). A similar comparison for sites before and after fledging showed that fighting increased at 35 sites and decreased at 10 ($P < 0.001$, binomial test). A combination of these two effects probably accounts for much of the correlation between date of hatching and incidence of fighting noted above. The rates of fighting were similar at sites where eggs or chicks had been lost and at sites where chicks had fledged, but there was generally less fighting at sites where no egg was laid (Table 18).

**Figure 46**
The relationship between the rate of arrival of prospectors at plot S1 and the rate at plot U. Data are from 4-h watches in 1977. Solid line shows the expected relationship if proportions of prospectors had been the same on both plots



During simultaneous watches at plots U and S1 the incidence of fighting was generally greater at U, with a higher number of fights per site on 14 out of 17 days ($P = 0.006$, binomial test). The rate of arrival of prospecting birds in relation to the number of sites was also higher at U than at S1 on all days. Despite the close inter-correlation between date, number of prospectors arriving, and number of fights, the higher incidence of both arrivals and fights at plot U suggests a causal relationship between these two parameters. Fluctuations in rates of arrival of prospectors and the frequency of fighting were closely correlated between the two plots (Figs. 46 and 47).

The incidence of fighting during the incubation period (July) showed relatively little diurnal variation, but during chick rearing (August) there were two peaks of fighting 12 h apart, at 0400 and 1600 h (Fig. 48), corresponding to peaks in the rate of arrival of prospectors. Rates of arrival in each 2-h period were significantly correlated with the number of fights during both incubation and chick rearing (Fig. 49) and this confirms the importance of arrivals in determining the incidence of fighting.

**Figure 47**
The relationship between the frequency of fighting at plot S1 and plot U. Data are from 4-h watches in 1977. Solid line shows the expected relationship if the incidence of fighting was the same on both plots

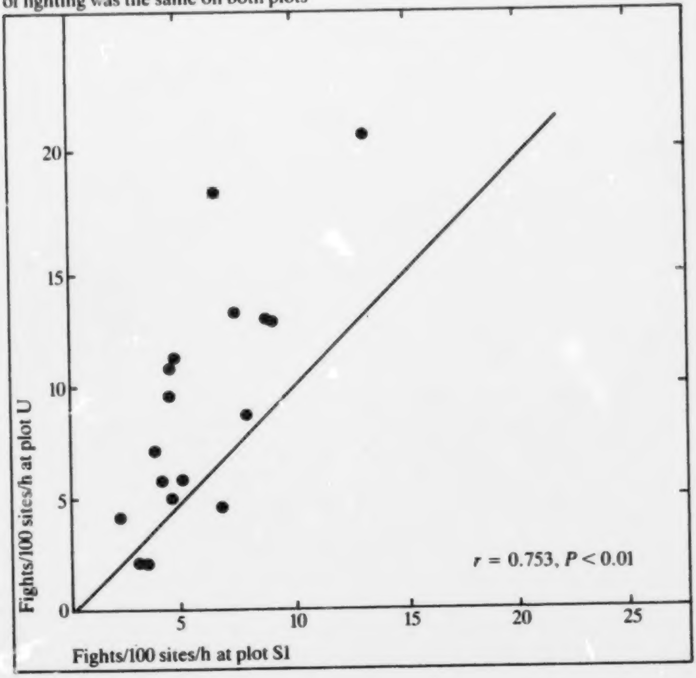


**Figure 48**
Mean numbers of fights per hour observed at plot S1 for six watches during incubation and five watches during chick rearing in 1975

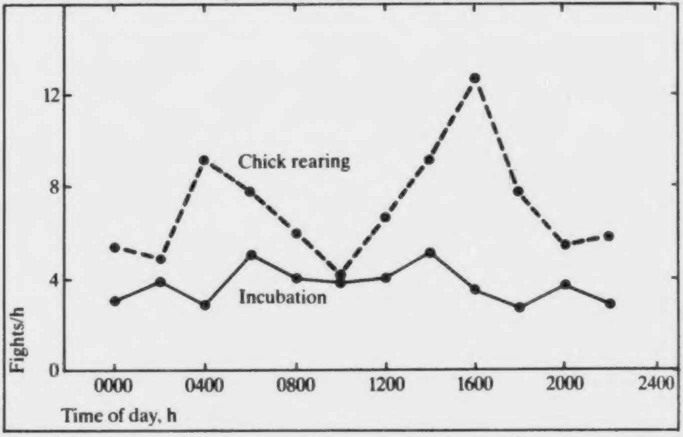
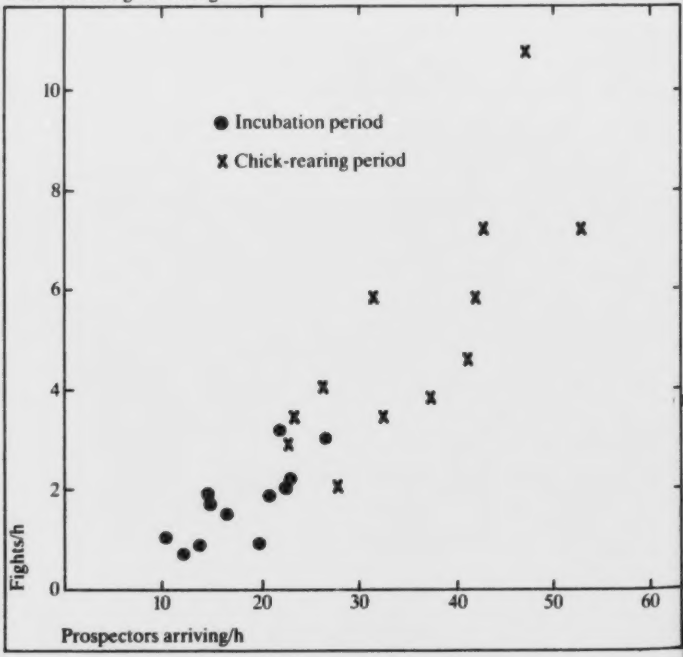


**Figure 49**
Frequency of fights at plot S1 in relation to the number of prospectors arriving. Data used are given in Figure 48



## 4.7. Factors determining seasonal changes in patterns of behaviour

The behaviour of both site-holders and prospectors suggests a trend of increasing attendance at the colony during the summer. During the pre-laying period most of the birds visiting the colony are apparently breeders with established sites. We observed no movements between different parts of the cliffs and all birds were in areas where we subsequently observed egg laying.

During July a steady increase in the rate of incubation exchanges and the amount of time spent at the site by both members of the pair suggest that birds have increasing amounts of time to spare after taking care of their own maintenance requirements. The pattern of incubation probably comes gradually to approximate the 12 h alternation found after hatching. Any increase in the rate of exchanges beyond the level of two-a-day presumably indicates that off-duty birds are visiting the colony during their off-duty period, suggesting that food is relatively abundant then.

Because the increase in daily counts during July and August is largely determined by the increased attendance of prospectors, either (1) more prospectors are arriving in the vicinity of the colony or (2) those that are present are spending more time on the cliffs. Changes in the behaviour of prospectors observed in July support the first effect, but both seem to be operating. In the first case, changing conditions make it possible for birds that had not previously done so to visit the colony; and in the second, that prospectors, like breeders, can spare increasing amounts of time for visiting the colony.

A general hypothesis which accounts for all these phenomena is that the availability of food for birds visiting the colony increases during the season. The increase may be due to an increased density or availability (including catchability) of prey within the same foraging range, or to a change in the distribution of prey, reducing the mean travel time between the colony and the foraging area. This hypothesis also explains some of the differences observed between attendance patterns in 1976 and 1977.

Daily counts during the pre-laying period were lower in 1977 than in 1976 up until 25 June. After the beginning of July, however, counts were consistently higher in 1977. Eggs were smaller and laid later in 1977 than in 1976 which suggests that food was relatively scarce during the pre-laying period in 1977. The frequency of feeding visits and the rate of growth of chicks, however, suggested that by late July and August food was more abundant in 1977 than in 1976 (Chapter IV). The relationship between predictions of the availability of food based on laying dates, and chick growth and the differences in the number of birds attending the colony supports the hypothesis that the level of attendance at the colony indicates the relative availability of food. The typical pattern of increasing attendance during the course of the summer therefore is primarily determined by changes in the numbers and/or distribution of prey organisms which follow a similar pattern from year to year.

Under this hypothesis changes in weather conditions during the season contribute only second-order variation in attendance patterns. Weather conditions may affect the murres' ability to find food or to land on the cliffs, which in turn affects attendance. During periods of high winds and low visibility birds commonly landed badly, cannoning into rock faces. Other birds landed carrying fish, wandered around the plot for a few minutes and then took off again, having apparently landed in the wrong place. Adverse conditions may limit prospectors even more from visiting the colony. Except under very extreme conditions as on 19 August 1977, there was no evidence that weather affected the rate of provisioning of chicks and, therefore, feeding is relatively unaffected by weather during the chick-rearing period.

During the pre-laying period weather conditions have a considerable effect in determining the number of birds attending the colony. At this period many birds are feeding along the edge of land-fast ice and Bradstreet (1977) has shown that the attractiveness of this feeding zone is considerably affected by wind speed and direction. Changes in attendance in relation to weather conditions during the pre-laying period may therefore be mediated mainly through the effects of weather on feeding success. The strong correlation between the magnitude of changes in barometric pressure and numbers of birds attending the colony suggests that murres are capable of perceiving such changes and may use them to predict weather conditions affecting feeding success. Otherwise, it is hard to imagine why they should respond to changes in pressure.

The important role of prospecting birds in determining levels of attendance suggests that there should be a correlation between the proportion of these "unattached" birds at the colony and the variability of daily counts. When the attendance of prospectors is highest (the first half of August), however, the variability of daily counts is actually at a minimum (this chapter, section 3.2); this may be partly explained by the fact that after early August, all the birds that will visit the cliffs that season have arrived, causing numbers to stabilize. It also suggests that food supplies are most stable at this time and it seems logical that the breeding of the murres should be timed so that chicks are being fed when the food supply is most predictable.

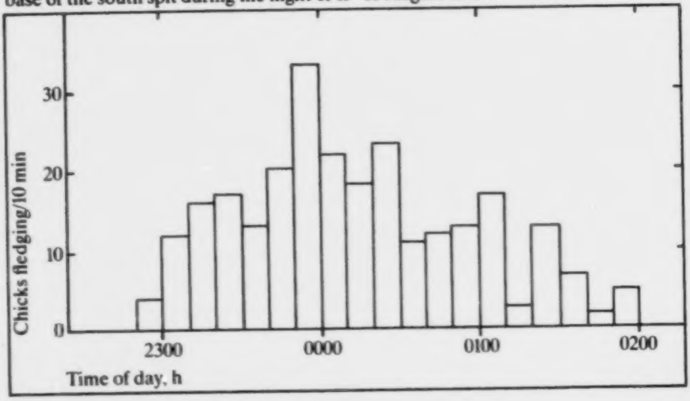
### 4.8. Behaviour at fledging

Fledging was observed only between 1610 and 0300 h. During the early part of the fledging period most chicks left the cliffs between 2200 and 0200 h, the period of lowest light (Fig. 50). On 22 August 1977, however, 59% ($N = 41$) of fledgings at plot S1 took place between 1600 and 2000 h, with a peak of 37% between 1700 and 1800 h. On this night 28% of all the chicks fledged from study plots that year left the cliffs, having been held up by adverse weather conditions during the previous few days (see Chapter III, section 2.3).

The behaviour of the chicks and their parents changed in the last few days before fledging. The parents brooded their chicks less; they stood up and sometimes moved 10–20 cm away from their sites, while the chicks made frequent bursts of wing flapping. Chicks about to fledge gave a loud, disyllabic call, "piu-piu", not heard otherwise and this usually indicated that the chick would fledge that night. The parent gave "arrr" calls intermittently, similar to those made during the arrival ceremony. Both of these calls increased in volume and frequency immediately prior to fledging.

The exact sequence of events at fledging varied considerably. Usually the chick approached the edge of the ledge several times and looked over, returning to its site in between. Sometimes the parent

**Figure 50**
Numbers of chicks observed fledging per 10-min period from cliffs visible from the base of the south spit during the night of 15–16 August 1975



followed the chick, but otherwise it remained sitting on the site. The chick did not leave its ledge unless its parent was beside it. At the edge of the ledge the chick "bowed", usually more frequently just before it plunged into the air. It flapped its wings vigorously at take-off, but ceased to do so once it was clear of the cliff and glided steeply downwards with wings and feet fully spread, levelling out sharply just above the water so that it sometimes bounced along the surface after landing. The parent jumped immediately after the chick and glided within 5–10 cm of its tail all the way to the sea. Up to five prospecting birds or site-holders without chicks usually accompanied the chick to the sea, but after landing the group quickly dispersed, leaving the chick with a single adult. The following extracts from field notes illustrate the variation in chick behaviour at fledging.

(1) *17 August 1976, plot G4, 2245 h*. Chick had been standing facing the sea for 4 min, parent sitting immobile beside it and facing the cliff. Chick made a few intention movements, bowing towards the sea, parent became alert, allopreened chick on head a few times, then chick jumped. (AJG)

(2) *17 August 1977, plot S1, 2250 h*. Both adult and chick giving high pitched strong vocalizations. Adult on inside of ledge keeping chick on outside. Several low-key calls between adult and chick. Chick then walked along ledge with adult following. Adult's movements forced chick to continue along ledge for ca. 3–4 m to a steep open edge towards the extreme left of the plot. Once at edge chick jumped off in a dive with little hesitation and the adult followed immediately leaving a 2–3 m separation between them. Total time from first identification (by calls) to actual departure about 5 min. (DNN)

(3) *20 August 1977, plot S1, 2320 h*. Both parents present. Chick repeatedly walks out to edge of ledge. Parent slowly leads chick over to extreme left edge of plot, successfully jumping a

large crack. Other parent showed no great interest. Chick jumps, followed by two prospectors. (S. Tingley)

(4) *22 August 1977, plot S1, 1823 h.* Adult leads chick to left side of plot. Parent and chick stumble across crack, chick hangs on, but parent falls off. Chick calls frantically, harassed by several other adults that had followed it across the plot. Chick jumps at 1834 h, followed by two prospectors. (S. Tingley)

(5) *26 August 1977, plot S1, 2139 h.* Chick walking back and forth at the edge of the ledge for 1/2 h. Adult began to give "arrr" call, leaning forward in front of the chick with the bill pointing obliquely downwards. Five minutes after adult began to call chick jumped. Adult returns 1 min later, then leaves after 20 s, 2 min later returns again, peers over the edge of the ledge and gives "arrr" call (the chick had clearly become separated from the parent during the descent). (AJG)

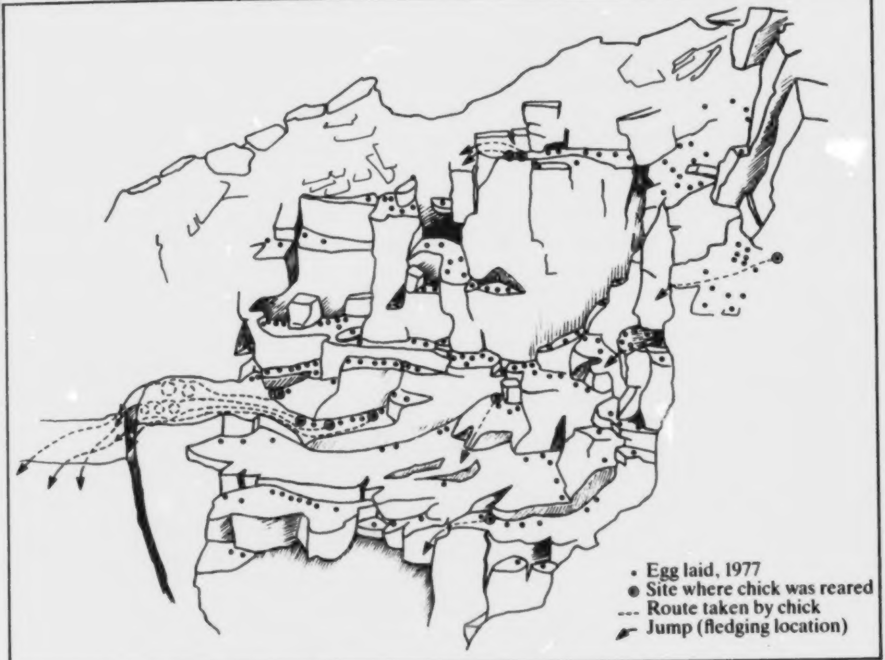
Chicks walked up to 10 m to reach a suitable launching spot. In some cases the parent appeared to lead the chick, but in others it remained close behind, giving regular "arrr" calls. Some routes taken by chicks on plot S1 are shown in Figure 51. Other adults frequently pecked at the chick and the accompanying adult. In one case, where a chick was left unattended, an adult, probably from a failed site nearby, approached the chick and pecked it so hard that it fell off the ledge.

Some chicks, particularly at plot S1, struck lower ledges immediately after take-off. When this happened the parent usually continued towards the sea and contact between the two was lost. The chick normally picked itself up and jumped again from the lower ledge, but in most cases an adult, presumably the parent, returned to the site within a few minutes. Chicks without adults were frequently seen on the water at the foot of the cliffs and these gave the "piu-piu" call continuously. Sometimes apparent reunions were seen where an adult rushed to a chick giving the "arrr" call loudly and both then swam off together without calling. Despite the very large number of birds present, parents and chicks were able to distinguish one another on the basis of vocalisations, as found by Tschanz (1959) and Schommer and Tschanz (1975) for the Common Murre.

Because of the timing of fledging it seems reasonable to assume that in most cases the parent accompanying the chick was the male. Scott (1973) and Birkhead (1976*a*) observed that the male accompanies the chick at fledging in the Common Murre and Bradstreet (1976) found that Thick-billed Murres accompanying chicks at sea were also males (of 47 chick–parent pairs collected, 46 adults were male). In most cases only one parent was present when the chick fledged, but on one occasion a bird which had just arrived with a fish and attempted unsuccessfully to feed the chick did not accompany it when it fledged, although the brooding parent and several other birds left simultaneously.

Chicks that landed on the beach or on ice pans floating offshore were sometimes killed by Glaucous Gulls. The parent usually landed on the sea nearby and immediately scrambled out to reach the chick. The few observed attempts at predation made after the parent had joined the chick were easily repulsed by the parent. Adults did not

**Figure 51**
Sketch of plot S1 showing the routes taken by some chicks which did not fledge directly from their sites in 1977 (drawn from study plot photo, App. 1)



accompany the few chicks we saw taken from the water by gulls. Chicks that had lost contact with their parent were most subject to predation and these would probably have died in any case. Mortality at fledging is nevertheless heavy and may be 30% of chicks fledging at certain plots (Chapter III, section 3). Greenwood (1964) observed that 11% of Common Murre chicks fledged at Handa, Scotland, lost contact with their parents at time of fledging and concluded that those chicks would probably not survive.

Synchronization between chick and parent is clearly crucial to the success of fledging and both parties must be in the correct state for it to take place. The decision of the chick is presumably based on an assessment of its physical maturity and it is interesting to speculate that the parent's input may be in monitoring the external environment and assessing conditions such as wind speed. A combination of these two evaluations would presumably provide a better decision than a unilateral action by either party. The potential for parent–offspring conflict is certainly present (Trivers 1974), and probably expresses itself in the case of chicks hatching late in the season, where the consequent delays in the departure of the parents may influence their subsequent survival.

### 4.9. Role of the sexes in the breeding cycle

During the pre-laying period it was rare for more than half of the breeding population to be present on the cliffs. The correlation between the number of birds present and the number of copulations per 100 birds suggests that during periods when numbers were low, most of the birds present may have been of the same sex. The fact that attempted copulations were more common relative to copulations when numbers were low suggests that males predominated during these periods and attempted copulations may have mainly involved birds whose mate was absent from the colony. The preponderance of males arriving prior to copulation can be explained if, during periods when females are present at the colony, males tend to remain on the water most of the time, visiting the cliffs periodically to copulate.

During the period when they are forming eggs, females probably require more time for feeding than males. The fact that about 13 days elapse between the loss of an egg and re-laying (Chapter III, section 2.1) indicates that a considerable time is required to accumulate sufficient energy reserves to lay. Thus, sites are occupied mainly by males during this period probably because females have to spend most of the time feeding.

Surprisingly, collections of Thick-billed Murres made in June at the edges of land-fast ice in Barrow Strait by Bradstreet (1977) contained significantly more males. A large proportion of the Prince Leopold Island population is believed to have been feeding along these ice edges during the pre-laying period. The majority of Bradstreet's birds, however, were collected between 20 and 25 June, the first 6 days of egg laying, and many females must have left for the colony by this time. The preponderance of males was greatest on 22 and 23 June (83%, $N = 35$, $P < 0.001$, binomial test), the first 2 days of heavy egg laying in the 1976 season. This may indicate that males leave the vicinity of the colony to feed during laying, building up reserves to undertake their first, prolonged incubation stint.

We did not study the role of the sexes in the establishment and defence of sites. But, if males spend more time at the colony during the pre-laying period, they may take a more active role in acquiring the site. During incubation and chick rearing, rates of fighting do not vary significantly between periods when males and females predominate, which suggests that the sexes share equally in the defence of the site during this part of the season. After fledging, females remain at the site for up to 20 days and during this period the incidence of fighting is high, particularly at sites without chicks and presumably occupied by females.

A roughly 12-h alternation of the sexes apparently becomes established at least by July and continues until the chicks fledge. The cycle is necessary during chick rearing to ensure that the male is present at the time of day when the chicks fledge, but the factors maintaining it during incubation are not clear. The alternation of the sexes explains the observation of several investigators that collections made at Thick-billed Murre colonies during the breeding season often have a strongly biased sex ratio (Krasovski 1937, Uspenski 1941, Kaftanovskii 1951). A collection made by Uspenski (1956), which yielded an equal sex ratio, may have been spread over the entire day.

### 4.10. Predation and anti-predator behaviour

Glaucous Gulls are practically the only predators of Thick-billed Murres on Prince Leopold Island, taking eggs and chicks and sometimes killing adult murres injured in rock-falls. Gulls used two distinct tactics when robbing murres of eggs or chicks:

(1) the gull approached an incubating or brooding murre on foot and molested it until the egg or chick was exposed long enough for the gull to snatch it; and

(2) the gull swooped unexpectedly, catching an adult murre by the tail or the wing tip and dragging it off the ledge, then circled to take the egg or chick before the murre could return to its site.

Sites on broad, sparsely populated ledges, where gulls could land and approach unmolested, were vulnerable to the first type of predation. Those on narrow ledges or the seaward edge of broad ledges and in situations where the gulls could easily manoeuvre close to the cliff were vulnerable to the second type.

At the approach of a gull, either on foot or in flight, murres made a sharp "uggah" (Pennycuick 1956) or "owka" (Tuck 1961) call, repeated while bobbing the head up and down. Site-holders became immediately alert when this call was given in their vicinity, stretching their necks up and turning the head from side to side to locate the source of alarm. Once the gull entered the plot the murres became silent and prospecting birds often left the cliff. Incubating or brooding adults kept their bills pointing towards the gull when approached, and where several sites were situated close together the resulting defence was very effective. Sometimes adults without chicks lunged at the gull, hurling themselves off the cliff at the same time, and this resulted in the gull flying off on several occasions. Three of the birds seen acting this way were site-holders that had lost their own chick. In two cases brooding birds actually grappled the gull with their bills, leaving their site in the process and on both occasions their chick took shelter under a neighbouring adult. The chicks returned to their parent as soon as it gave the "arrr" call, following the departure of the gull. Only one of more than 10 attempts of this type that we witnessed during the study resulted in a successful predation.

The tactic of pulling adults off the ledge was much more successful than the direct confrontation; out of four attempts seen all resulted in successful predations, but only a few "specialist" gulls used it. In 1975 regular collections of eggshells around the nest of such a gull yielded 300 between 10 and 25 July. The technique may also have been partly dependent on weather conditions. In 1977 the tactic was seen twice at plot U on 18 July during strong easterly winds, which caused fierce updraughts. The gull involved took advantage of these updraughts to hover beside ledges which would probably not have been accessible otherwise. Seven eggs from this plot disappeared in 2 days of strong winds, but only one more egg was lost in that season.

Some examples of interactions between gulls and murres at plot S1, taken from field notes, illustrate the effectiveness of joint defence by murres:

(1) *7 July 1975, 2240 h*. Gull appears at the left-hand side of plot, moves towards egg (site 129). The whole plot falls silent and all bills turn towards the gull, following it with necks stretched

One bird hurls itself towards the gull, which flies off, followed by the murre which soon returns. It is a site-holder which has just lost an egg. (AJG)

(2) *2 July 1975, 2200 h*. Gull enters plot at left-hand side. All murres within 3 m crane their necks towards it, many giving alarm ("owka") cries. Murre on site 152 has a short fight (with the gull), with vigorous pecking by both birds. The gull stepped back and the murre rolled its egg 10 cm up the slope to a more protected position. The gull next attacked the murre on site 138, grabbing it by the wing and pulling it off its egg. Both birds peck wildly. The murre escapes and returns to its egg. This occurs several times and at 2218 h the egg is dislodged and rolls off the ledge. The attack continues and at 2220 h the murre falls off the ledge. The gull then attacks the bird at site 197, pulling it off its egg by the tail. Bird at site 138 returns and attacks the gull again, but again falls off the ledge, looking battered. The attack at site 197 is resumed, the gull pulls the bird off the egg by the tail several times, but at 2232 h it leaves without having obtained any food. (R. Forbes)

(3) *13 July 1975, 0140 h*. Male gull from nest 16 enters the plot from the left, fences and bills with bird at site 148, but is pecked up the rump by bird at site 147. It then clashes bills with bird at site 219 and flies off. (AJG)

The degree of predation by Glaucous Gulls can be estimated from the number of murre eggs collected at gull nest sites. From 10 to 26 July 1975 three nests yielded 39, 44, and 300 eggshells, respectively (Table 19), and another yielded 105 at a single collection on 31 July. The nest at "R" may have been exceptional. Gull chicks began to hatch only about the first week of July and before this time the number of eggs eaten by adults could not be counted as many would have been devoured away from the nest. After 25 July, as murres began to hatch, the number of murre eggs found at gull nests fell off sharply and this may indicate a rapid switch to chicks, which became very numerous in gull pellets at the same time.

We estimate that the 22 gull pairs nesting at the top of cliffs took an average of at least 50 eggs per nest during 10–26 July 1975. Eggs apparently were less important to the diet of 28 gull pairs nesting at the base of the cliffs, and we therefore estimate that they took 25 eggs per nest. We therefore estimate that a minimum of 1800 murre eggs were lost to predation by Glaucous Gulls during this period. Estimating losses during 1–10 and 26–31 July at half this rate gives a total estimate of 2700 eggs removed by gulls over the whole season, most of them after the date when re-laying has ceased (Chapter III, section 2). This is about 4% of the eggs laid and 15–25% of all egg mortality based on a population of 71 000 pairs (this chapter, section 5) on the east cliffs.

The estimate for the number of eggs taken during 10–25 July (1800) represents a rate of 0.16% per day. A rough check on the validity of this estimate is provided by 24-h watches at plots S1 and S2 on 3 days during this period in 1975. We observed three predations by gulls among 250 eggs under observation, giving a rate of 0.4% per day. The plots involved were near the top of the cliff and close to the

**Table 19**
Number of eggshells of Thick-billed Murres collected at nest-sites of three pairs of Glaucous Gulls located at the top of the cliffs during 1975

| | No. of murre eggs collected | | | |
|---|---|---|---|---|
| | Gull nest no. and location | | | |
| Date | 12 (S) | 13 (S) | 15 (R) | Total |
| 10 July | 5 | 2 | 18 | 25 |
| 11 | 3 | 1 | 17 | 21 |
| 12 | 1 | 3 | 29 | 33 |
| 13 | 1 | 1 | 25 | 27 |
| 14 | 6 | 1 | 26 | 33 |
| 15 | 3 | 6 | 25 | 34 |
| 16 | 0 | 0 | 19 | 19 |
| 17 | 4 | 5 | 19 | 28 |
| 18 | 2 | 2 | 24 | 28 |
| 19 | 4 | 0 | 26 | 30 |
| 20 | 2 | 3 | 6 | 11 |
| 21 | 4 | 3 | 23 | 30 |
| 22 | 2 | 7 | 25 | 34 |
| 23 | 0 | 7 | 12 | 19 |
| 24–26 | 2 | 3 | 6 | 11 |
| 27 | 3 | 1 | 4 | 8 |
| 28 | 0 | 0 | 2 | 2 |
| 29–31 | 0 | 0 | 0 | 0 |
| 1–7 August | 0 | 0 | 1 | 1 |
| Totals (10–26 July) | 39 | 44 | 300 | 383 |
| Totals (10 July – 7 August) | 42 | 45 | 307 | 394 |

"specialist" nest at R and may have suffered unusually high predation, but the order of magnitude appears to be correct.

Although the rate at which chicks were taken could not be quantified, the food requirements of nestling gulls must increase as the season progresses. If chicks are removed at the same rate as eggs, then about 3% are probably taken, comprising 25–40% of pre-fledging chick mortality. Thus, Glaucous Gulls are almost certainly the most important source of reproductive failure for murres at Prince Leopold Island and their activities are sufficient to account for some of the differences in breeding success observed between different types of breeding site (Chapter III, section 4.2).

# 5. Census and population size

## 5.1. Methods

The implications of observed attendance patterns for methods of monitoring population changes between years have already been discussed (this chapter, section 3.4). For many purposes it is useful not only to monitor changes, but also to obtain a complete census of the breeding population. This allows recruitment to be estimated and compared with observations on mortality to assess the impact of new causes of mortality on the population. A complete census also makes it possible to estimate the importance of the species within the local food web.

Adequate methods for accurately censusing large seabird colonies, such as Prince Leopold Island, are only now being developed. The principal problems encountered at this type of colony are as follows:

(1) There are too many birds present for one or two observers to be able to count them all within a single day.
(2) Some parts of the colony are visible only from the sea, and from a small boat it is almost impossible to count birds high up on the cliffs because of the difficulty of keeping track of which areas have been counted.
(3) Areas visible from the top of the cliff cannot all be viewed from the same vantage point and there can be difficulty in identifying the boundaries of areas already counted. This problem is particularly acute when areas counted from the cliffs adjoin areas which have to be counted from a boat.

Counts of the total numbers of birds present on the cliffs can be converted to estimates of the numbers of breeding pairs by using *k* (Gibson 1950, Brun 1969, Nettleship 1976, Birkhead and Nettleship 1980) where:

$$k(t_1) = \frac{\text{No. of first eggs laid on the study plots}}{\text{Total no. of birds present on study plots at time } t_1}$$

Because census counts extended over several hours in many cases, it was not possible to make counts at study plots and census areas completely simultaneous. Instead, the study plots were counted every 3 h during the census and the *k* value used was the mean of those recorded at the start and finish of each 3-h period.

We photographed areas that were not visible from the cliff top, from a boat about 300 m offshore. Counts were made subsequently from 28 × 40 cm glossy black-and-white enlargements. Observers on the cliffs counted birds at the study plots at the same time that the photographs were taken.

We used a spotting scope and a hand counter for direct counts. Large areas of cliff were divided into smaller units (on Polaroid photographs taken at the time of census), which were then counted separately. All observers involved in census counts had considerable experience in counting murres and sample counts were recounted by a different observer.

**Table 20**
Comparisons of direct and photographic counts made on 9 August 1975 at Prince Leopold Island

| Area location | Direct count | Photo count |
|---|---|---|
| Ld | 1955 | 1972 |
| Le | 1773 | 1831 |
| Lf | 1165 | 1232 |
| Totals | 4893 | 5035 |

The accuracy of the methods used to estimate the number of breeding pairs depend on the following factors:

(1) the accuracy of the counts (direct and photographic),
(2) the accuracy of the method used to determine breeding,
(3) the proportion of the total colony represented by the study plots, and
(4) whether the *k* ratio observed on the study plots is representative of the entire colony.

Comparison of replicate counts by experienced observers over areas containing about 1000 birds suggest that discrepancies of up to 5% can be expected. Arrivals and departures take place constantly, however, and not all of the differences observed constitute counting errors. A comparison of direct and photographic counts made in 1975 showed that, for good quality photographs, counts were very similar, although photographic counts tended to be slightly higher ( Table 20). This finding is contrary to the results of similar comparisons made by Harris and Lloyd (1977), who found that counts made from photographs consistently underestimated the numbers of birds present. The difference may be explained by the fact that all counts given here were made by S. Tingley, an experienced photo analyst, who was engaged in making photographic counts of murres on a full-time basis. Where the quality of the photographs is poor, the reliability of photographic counts falls sharply.

The study plots represented less than 1% of the total population of the East Cliff colony. Although they were scattered over the full length of the cliffs they were not a random sample, since they were chosen for convenience of observation and were therefore all situated on the upper third of the cliffs, mainly at the top. This problem was unavoidable and possible biases which it introduced could not be measured.

The quality of photographs used for counting varied considerably between different areas and between years. The final estimate of the breeding population is based on photographs taken in 1976, supplemented by a few taken in 1977. Direct counts included, however, are those made in 1977, because not all areas visible from the top of the cliff were counted in 1976.

## 5.2. Results

The area of cliffs bounded on the south by point E and on the north by point I (Fig. 8) was almost all visible from the top of the cliffs and this area was counted completely in all 3 years (Table 21). The difference between the maximum (1976) and minimum (1977) estimates for the breeding population was approximately 7% of the mean estimate, which may give an indication of the limits of accuracy of the method.

We estimate the total number of breeding pairs on the East Cliff colony at 71 000, with a further 15 000 pairs at the North Spit colony, giving a total estimate for the entire island of 86 000 pairs (Table 22).

Tingley, who performed the photo counts for 1976 and 1977, ranked the quality of the photographs on a five-point scale. Those classified as "good" were equivalent in quality to those used for the comparison of photo and direct counts in Table 22, and all were of better quality than the worst included in the 1975 census. Counts from "poor" photographs, however, probably underestimated the number of birds present and this involved 34% of the birds counted by this method. Assuming a maximum error of 50% due to the quality of photos used then our final estimate may have been too low, by as much as 8000 pairs. Adding a further 5% margin to the overall estimate

**Table 21**
Comparison of the results of direct counts made on the area of cliffs between E and I (Fig. 8) in 1975–77

| Year | No. of birds | Estimated no. of breeding pairs |
|---|---|---|
| 1975 | 32 958 | 24 090 |
| 1976 | 33 359 | 25 620 |
| 1977* | 32 469 | 23 854 |
| Mean | | 24 521 |

* Includes 750 birds counted from a photograph taken in 1976.

**Table 22**
Comparison of a preliminary analysis of population made in 1975 using limited information (direct counts and a poor quality set of photographs) and a detailed census performed in 1976 and 1977. (See Figure 8 for location of points)

| Area of cliff | No. of breeding pairs | | Census technique |
|---|---|---|---|
| | 1975 | 1976–77 | |
| East Cliff colony | | | |
| South spit to E | 6 840* | 15 225 | Photo |
| E to I | 24 090 | 23 854 | Direct count |
| I to P | 10 290† | 8 177 | 1975 direct/photo<br>1976/77 photo |
| P to S | 12 379 | 13 887 | Direct & photo |
| S to Z | 10 266 | 10 046 | Direct & photo |
| Totals | 63 865 | 71 189 | |
| Totals excluding south spit to E area | 57 025 | 55 964 | |
| North Spit colony Totals | 6 536* | 15 114 | Photo |
| Grand totals (entire island) | 70 401 | 86 303 | |

* Estimate based on analysis of poor set of photographs caused by fog.
† Subsequent re-analysis of data reveals that this figure almost certainly includes an observer recording error, which makes it too large by about 1000 pairs; the real value should be much closer to that made in 1976–77.

gives limits of 82 000 – 99 000 pairs; the true figure falling probably in the top half of this range.

If the greatly different 1975 and 1976–77 estimates for the North Spit colony and the area between the south spit and E on the east cliffs are excluded, the difference between the two total estimates is approximately 1300 pairs, only 2% of the mean. Details of counts and correction factors are given in Appendices 7 and 8.

To sum up, the results of these analyses of population between 1975 and 1977 indicate that the size of the breeding population (1977) is about 86 000 pairs (East Cliff colony, 71 000; North Spit colony, 15 000) with a range of 82 000 – 99 000 pairs.

## 6. Summary

(1) In 1976, the only year in which arrival at the colony was observed, Thick-billed Murres began to arrive at Prince Leopold Island in mid May, but large numbers did not appear until early June. That year ice in Lancaster Sound broke up relatively early.

(2) Attendance at the colony during the pre-laying period was characterized by extreme fluctuations in numbers, determined, in part, by weather conditions.

(3) From the start of egg laying onwards, numbers fluctuated much less and were only slightly influenced by weather, except under extreme conditions.

(4) In all 3 years numbers peaked in the first half of August, just before the start of fledging, and declined steeply thereafter.

(5) During the incubation period numbers were highest during the middle of the day, but during the chick-rearing period the peak came at 1800 h, becoming more pronounced towards the end of the season.

(6) Fluctuations occurring during July and the first half of August were determined largely by the numbers of prospecting birds present, which rose during the course of the season, a major influx occurring in all years in mid July. Overall numbers were closely correlated to the rate of arrival of prospecting birds landing on the cliffs.

(7) The ultimate factor determining the number of birds attending the colony appears to be the availability of food, and hence the amount of time that birds can spare from foraging to visit the cliffs. This explains why the numbers of birds counted in 1977 were consistently higher than in 1976, after the end of June, despite the fact that the number of eggs laid was almost identical.

(8) The number of visiting prospectors varies between different parts of the colony, causing differences in *k* ratios (number of breeding pairs/number of birds counted) and this may affect the interpretation of census results and the design of monitoring procedures.

(9) The incidence of fighting among birds on the cliffs increased throughout incubation and chick rearing, being highest when the rate of arrival of prospecting birds was high. Failed breeders were involved in fights more frequently than successful breeders and those with chicks more often than those with eggs.

(10) The duration of incubation stints decreased during the course of the season, from approximately 24 h at the time of laying to about 12 h by the time of hatching. The behaviour of breeding pairs during the chick-rearing period appears to be dominated by a 12-h alternation of the sexes. As a result, the majority of birds brooding chicks between 1800–0200 h are males, apparently to ensure that the male is present to accompany the chick at fledging.

(11) Fledging normally takes place during the hours of lowest light intensity, the chick being accompanied by the male parent. Synchronization of behaviour between parent and chick is important for successful fledging and chicks that become separated from their parent at this point probably do not survive long.

(12) Gull predation accounted for an estimated 15–25% of all egg loss in 1975. Two different techniques were employed by the gulls, one being much more successful than the other, but used by only a small number of specialists. Certain types of breeding sites appeared to be particularly vulnerable to gull predation.

(13) A census at the colony, conducted partly by direct counts and partly by photographic analysis, yielded an overall estimate of 86 000 breeding pairs of Thick-billed Murres on Prince Leopold Island.

# Chapter III Timing and success of reproduction

# 1. Introduction and methods

The reproductive rate of a population is one of its most important demographic parameters. Changes in reproductive success may result in alterations in the total size of the population. Even where the changes are counterbalanced by density-dependent selection later in the life cycle, they will still cause changes in the age-structure of the population, perhaps feeding back to further changes in reproductive success. Measurements of reproductive success are fundamental, therefore, to a proper understanding of population dynamics.

Much research has already been conducted on the reproductive ecology of seabirds, particularly those which nest in dense colonies, because it is relatively simple to obtain a large amount of information on these in a relatively short time. Consequently we could easily select those features of reproduction which could readily be measured and which could be expected to yield the maximum information on the causes of variation in reproductive success. We wanted not only to obtain the most accurate possible estimates of reproductive success for the Prince Leopold Island population, but also to evaluate the accuracy of our methods, the possible sources of error, and the best ways to make them comparable for different colonies, different types of breeding site, and different observers.

Timing of breeding of colonial seabirds is related to breeding success (Coulson and White 1958, Nettleship 1972, Davis 1975, Parsons 1975, Lloyd 1979). Apart from its relationship to reproductive output, information on the timing of breeding is crucial to any conservation strategy, since the feeding behaviour and foraging range of breeders will be determined partly by the stages of the breeding cycle. Thus we needed to know the within- and between-year variation that might be expected; to compare observations at Prince Leopold Island with those made at other colonies it was necessary to index events, such as changes in attendance, to the timing of laying or hatching. Information concerning factors which influence the timing of laying can be interpreted to throw light on the major constraints affecting reproduction and this in turn may be helpful in predicting the effect of environmental changes on the reproductive output of the population.

## 1.1. Methods and variables measured

We measured the following variables:

(1) timing and synchrony of egg laying,
(2) duration of the egg-laying period,
(3) length of the incubation period,
(4) length of the chick-rearing period,
(5) timing of replacement eggs,
(6) hatching success of first eggs and replacements (eggs hatched/ eggs laid),
(7) fledging success of first eggs and replacements (chicks fledged/ chicks hatched), and
(8) overall breeding success (chicks fledged, including relays/ first eggs laid).

We attempted to measure variation between different parts of the colony by comparing different study plots and variation between sites by comparing different types of sites. Inter-year variation was measured by comparing the 3 years of the study.

During the last week before egg laying, birds attending the colony sit on their sites in a posture indistinguishable from that adopted during incubation. A brief scan of the breeding ledges at this stage does not reveal which birds have already laid. Thus, most previous work on the timing and success of breeding in murres has been conducted by examining the breeding ledges at close quarters and disturbing the birds to see whether an egg or chick is present (e.g., Tuck 1961, Uspenski 1956, Swartz 1966, Johnson and West 1975).

This method introduces some biases, however. Many eggs and chicks are dislodged during the process by the rapid departure of their parents and it is unlikely that all the resulting mortality could be detected and taken into account. In addition, loose rocks, the position of which may determine the suitability of a site for nesting, are shifted by climbers and some types of sites (e.g., narrow sloping ledges) may be more affected than others. Since site characters are related to breeding success and timing of laying (see this chapter, section 4), further biases are introduced.

We used the technique developed by Birkhead (1976*a*) to study the breeding success of Common Murres *Uria aalge* on Skomer Island, Wales (see also Birkhead and Nettleship 1980). Sites are watched at a distance sufficient to ensure that the birds are not disturbed by the observer; in the case of Thick-billed Murres on Prince Leopold Island this minimum distance was about 6 m. Using designated study plots, each site where a bird was present regularly during the pre-laying period was mapped (1975) or marked on a photograph of the plot (1976, 1977) and numbered. The status of each site was recorded each time the plot was visited, using the following conventions:

o = no egg or chick present,
e = egg seen for the first time, i.e., the laying date,
e? = bird sitting, but egg not seen (used prior to laying),
√ = status apparently unchanged (for sites where an egg or chick had already been recorded),
√OK = status unchanged, egg or chick seen, and
C = chick recorded for the first time, i.e., the hatching date.

Where o was recorded one day and e the next, we knew the date of laying within 24 h (mean error 12 h). Where o, e? and e were recorded on successive days, we knew the date of laying within 48 h (mean error 24 h) and both of these categories were included in the analysis of laying dates. Dates of laying known less accurately were ignored.

No difference was found in the duration of incubation calculated for sites where the date of laying was known within 24 h and those where it was known within 48 h. This suggests that females may sit very tightly on their laying sites during the 24 h prior to laying. In 1977 the laying dates of 42% of first eggs ($N = 650$) were recorded within 48 h, but the proportion varied between plots, from 14% at Q1, the plot farthest from the observers, to 68% at U, the closest plot. Thick fog prevented observations at Q1 on several days during the laying period and contributed to the low success at determining dates of laying on that plot.

Detecting hatching was considerably easier than detecting laying. The chick is not usually brooded in the brood patch, but most commonly rests between the flank and the wing of its parent. Adults brooding in this way assume a characteristic pose, with one wing trailing on the ground, and the adoption of this posture and the presence of an egg-shell nearby were both useful clues that hatching had occurred. Egg-shells could be confidently used to indicate hatching at sites in isolated and low-density areas, but where sites were close together it was often not possible to tell which site the shells had come from. Adults brooding chicks shifted more frequently than those incubating eggs and the chicks often burrowed their bills through the feathers at the bend of their parent's wing so that the tip poked out.

In 1977 we recorded 94% of hatching to within 48 h, the proportion varying from 85% on plot N to 100% on plot Q4. Most chicks were detected within 24 h and the proportion would have been higher but for 2 days of thick fog during the hatching period. Chicks that disappear within 24 h of hatching go undetected and this error tends to increase apparent egg mortality and decrease apparent chick mortality. It does not, however, affect calculations of overall breeding success.

Fledging was simple to record in most cases because the adult attending the site intermittently after the chick had fledged did not normally assume the brooding position and the absence of the chick could therefore be detected immediately. Most fledging took place between 2000 and 0200 h and when we saw no chick in the morning we assumed it had fledged the previous night. We assumed that chicks which disappeared 15 days or more after hatching had fledged, and those which disappeared earlier had died. The rate of disappearance between 3 and 14 days after hatching was only 0.3% per day and the error introduced by possible misclassifications is therefore likely to be small. The ages of chicks actually seen fledging without disturbance in 1977 ranged from 16 to 25 days ($N = 35$).

The length of the incubation period was calculated by subtracting the date of laying (date when the egg was first seen) from the date of hatching (when the chick was first recorded). The length of the chick-rearing period was calculated by subtracting the date of hatching from the date on which the chick was first noted as absent.

The intensity of observations differed among seasons. In 1975 and 1976 two observers were available during the laying period, although in 1975 one of these had other commitments which reduced the daily work effort to 1.7 person-days. In 1977 three observers were available, though one worked only half-time. Approximately 14 person-hours per day were devoted to site checking in 1975 when 11 plots (G1, G4, M, N, Q1, Q4, S1, S2, S3, S4, U) were observed, but intensity was uneven, with observations concentrated on plots G1, G4, S1, and S2. Dense fog was very frequent during the laying period and badly hindered observations on plots M, N, Q1, Q4, S3, and S4. In 1976 16 person-hours daily were devoted more or less evenly to the same 11 plots, while in 1977 20 person-hours were devoted to seven plots, four of which (G1, G4, S1, U) were observed daily and the rest (N, Q1, Q4) less frequently.

In 1975 practically all laying dates recorded to within 48 h were on plot S1 ($N = 128$). In 1976 and 1977 the number of laying dates recorded to within 48 h was similar ($N = 288$ and 274, respectively), but accuracy appears to have been higher in 1977 (as judged from calculated incubation periods). In 1976, 17.1% of laying dates ($N = 246$) fell outside the range 29–36 days for incubation, and were therefore probably not correct to within 48 h, whereas in 1977 only 1.6% ($N = 186$) fell outside these limits. In 1976 two inexperienced observers had to become familiar with about 500 sites each and many of the mistakes made in that year probably resulted from the misidentification and confusion of site numbers. In 1977 two of the three observers had had previous experience of the study plots.

Appendix 9 gives data concerning timing and breeding performance for pairs on the study plots.

### 1.2. Discussion of methodology

Sightings of eggs depended on periodic movements of the incubating birds, which exposed the area beneath the brood patch. The presence of eggs could be detected with certainty more easily than their absence. The following factors influenced the ability of observers to detect eggs:

(1) the length of time spent observing the plot,
(2) the distance from the observer to the plot,
(3) the observer's previous experience,
(4) the topography of the plot and the dispersion of sites,
(5) weather conditions, and
(6) stage of incubation and time of day (probably).

To assess the ability of observers to detect eggs, three observers (BD, AJG, ST) watched plot S1 simultaneously for 2 h from 1530 h on 14 July 1977 without commenting to each other on what they observed. Each observer saw a similar number of eggs (55, 54, and 47) during that period, but combined they saw 75 different eggs, so that the best observer detected a maximum of 73% of the observed eggs. The plot was known to hold about 140 eggs on that date, so that 6 person-hours of observation detected only just over half of the eggs present. The rate at which eggs were detected rose initially, remained constant up to 50 min and then declined thereafter (Fig. 52).

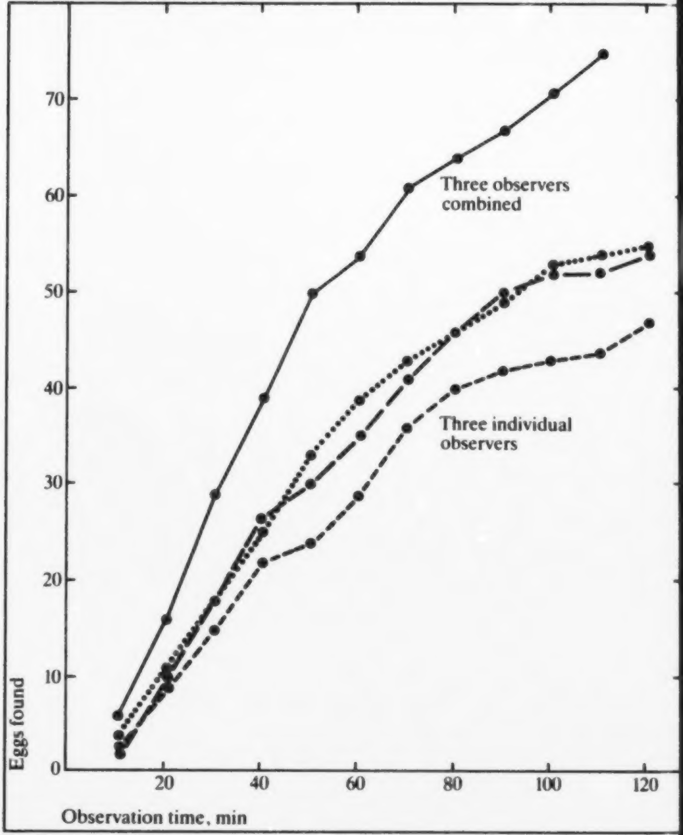
A comparison of two similar watches carried out by AJG at plot S1 on consecutive days (Fig. 53) shows the apparent effect of weather conditions on the detectability of eggs. In sunny conditions on 12 July 1977 31 eggs were seen in 70 min, while only 23 were seen in the same length of time on the preceding day when the sky was overcast. When the weather is warm the incubating birds seem to move about more frequently, thus exposing the eggs to view.

If the type of movements that expose the eggs occur independently at random intervals, then the relationship of the total number of eggs detected to the observation time can be predicted from the initial detection rate using the formula:

$$y = [1 - (1 - r/N)^{6x}] \times 100\%$$

where $y$ is the proportion of eggs that are detected in $x$ hours of observation, $r$ is the initial rate of detection per 10-min period and $N$

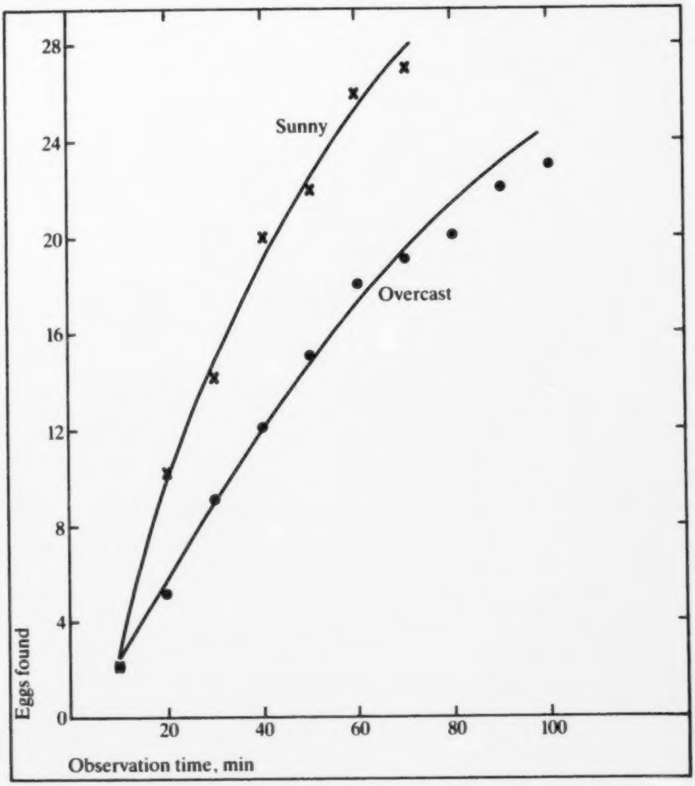
**Figure 52**
Cumulative plot of the numbers of new eggs seen per 10-min period by three observers watching plot S1 from 1530 h, 14 July 1977



the total number of eggs present. In practice, *r* was estimated as the mean of the number of eggs seen during each of the first three 10-min periods. For all observers combined on 14 July 1977, $r = 10$ and the equation predicts the discovery of 59% of eggs after 2 h, 83% after 4 h,and 97% after 8 h. This agrees quite closely with the actual discovery of 54% in 2 h. For a single observer working under sunny conditions, as on 12 July 1977, $r = 7$ and the formula predicts the discovery of 91.5% of eggs in 8 h. For 11 July 1977, $r = 4.5$ and the predicted proportion seen in 8 h is 77%.

If the observer can scan the entire plot simultaneously, the proportion of eggs found is independent of the number of sites on the plot, and hence up to a certain size of plot, efficiency, in terms of the number of eggs recorded, increases with the size of the plot. In practice the number of sites that gives maximum efficiency will be determined by the level of accuracy required. Laying dates can be

**Figure 53**
Cumulative plots of the number of new eggs seen per 10-min period by the same observer watching in overcast conditions from 1200 h, 11 July 1977 and in sunny conditions from 0930 h, 12 July 1977, plot S1



determined for a high proportion of the sites observed, and with the same amount of observer effort, only at the expense of the overall sample size. For instance, if an observer can see 70% of the eggs on 100 sites in 4 h and 90% in 8 h, then by watching two plots of 100 sites for 4 h each he can record 140 eggs against 90 detected by watching a single plot. The number of layings recorded within 24 h will be 98 and 81 respectively, although in the case of the two plots this constitutes only 49% of all layings against 81% on the single plot. The exact apportionment of effort will depend on the objectives of the study.

For plots too far away to be scanned with the naked eye, the number of sites monitored simultaneously is determined by the number falling within the field of view of the binoculars or telescope and this must reduce efficiency. The distribution of sites is also important because sites that are spaced out will be more difficult to scan than sites which are close together.

The previous experience of the observer is important in determining ability at egg-detection. If the observer knew and memorized the site numbers, the sightings could be recorded quickly, but if it was necessary to consult a map or photograph to find the number of the site, attention was diverted from the plot and eggs were probably missed. Inexperienced observers were unable to tell which behaviour on the part of sitting birds was likely to precede their standing up and, hence, they did not concentrate their attention in the most efficient manner. All observers agreed that their ability to detect eggs improved with practice, but the difference was not quantified.

If the eggs recorded each day constituted a random sample of those present, then the number of times that each was recorded before hatching should follow a Poisson distribution, but this was not the case (Fig. 54), suggesting that sites probably vary in the ease with which eggs can be detected.

**Figure 54**
Distribution of the number of days on which eggs were definitely observed during the incubation period at plot S1 (light line), compared with the Poisson distribution (bold line) for the same mean

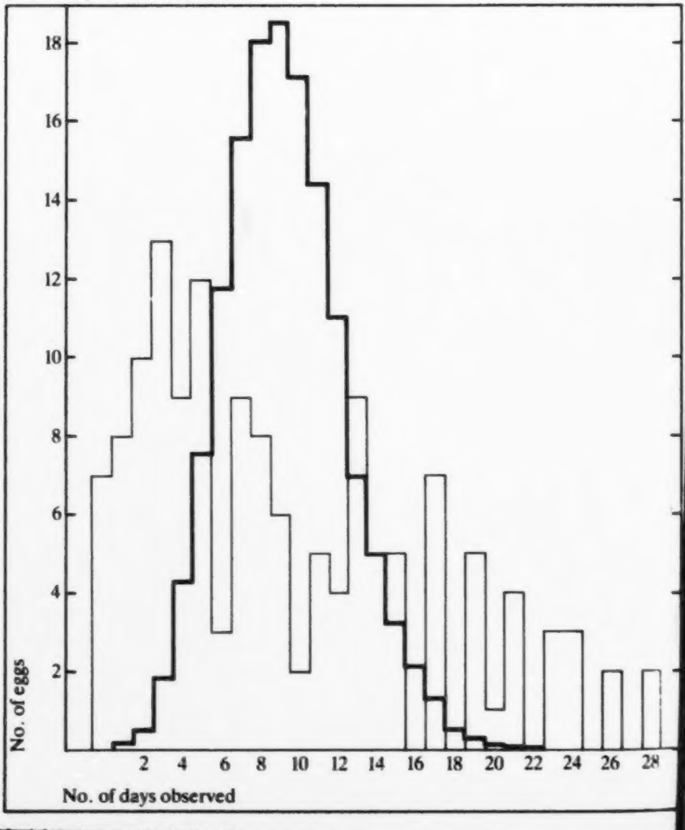


**Table 23**
Comparison of observed dates of laying with those estimated from observed dates of hatching (using an incubation period of 32 days) for plot S1 in 1976

| | Dates of laying | | | | |
|---|---|---|---|---|---|
| | 20–23 June | 24–27 June | 28 June – 1 July | 2–5 July | 6–9 July |
| Observed | 11 | 24 | 10 | 16 | 5 |
| Calculated | 12 | 39 | 39 | 20 | 7 |
| Obs./Calc. × 100% | 92 | 62 | 26 | 80 | 71 |

Eggs could be detected more easily at some sites, such as those which were isolated and without protection from nearby rock faces, particularly where the birds sat sideways to the observer, than at others. Where eggs were hidden behind other birds or in crevices detection was difficult, sometimes impossible.

Because eggs could be detected more easily on some types of sites than on others, sites for which accurate laying dates were obtained did not constitute a random sample of those observed, possibly causing a bias in overall estimates of laying dates. Another and probably more important source of bias was the fact that early and late layings could be detected more easily than those which occurred at the peak of laying. At the start of the laying period, particularly when winds were high, many sites were not occupied and attention could therefore be concentrated on the remaining birds. Towards the end of the laying period, by which time most eggs had been detected, attention could be concentrated on the few sites still in doubt. The result of these two effects was to increase the variance in laying dates based on those observed within 48 h, compared with the actual situation. A comparison of observed laying dates on plot S1 in 1976 with laying dates calculated from observed hatching dates illustrates this effect (Table 23). The proportion of layings recorded within 48 h during the first 4 days of laying (92%) was considerably higher than the proportion recorded in the middle of the period (26%).

Another source of bias in recording laying and breeding success is the fact that loss of eggs is high immediately after laying (7% of eggs were lost in the first 2 days after laying in 1977, see this chapter, section 3.1). Since plots were only visited once daily, many eggs laid and lost within 24 h were probably not detected. If the egg was replaced, then the replacement egg was recorded incorrectly as a first egg; if a replacement egg was not laid, then the pair occupying the site was recorded as not having attempted to reproduce. If the chance of a replacement egg being lost is independent of the loss of the first egg, then the chance of both eggs going undetected is very small (<1%), but later eggs are less likely to be relaid than early eggs. This weakness applies to any method for which sites are not kept under observation continuously throughout the laying period (clearly an impossible task), but is particularly acute for sites where detecting the eggs is difficult. If more eggs are lost from these sites without being detected than from more exposed sites, then their apparent breeding success will be biased upwards. If the intensity of observation differs between plots, then this effect will cause differences in their apparent breeding success, and in any case all observed figures for breeding success are likely to be higher than the actual figures.

We hope to standardize techniques developed in the present study to provide long-term monitoring of changes in the recruitment rates of Thick-billed Murres at Prince Leopold Island and elsewhere, and it is therefore important to evaluate the effectiveness of the methods used. Several factors seem likely to affect the comparability of results obtained at other colonies:

(1) the intensity of observations and the experience of the observers,
(2) the distances from observation points to plots and the topography of the plots, and
(3) colony-specific differences in behaviour (e.g., diurnal patterns of attendance may be more marked in colonies at lower latitudes; see Tuck 1961 and Birkhead 1976*a*, 1978*b*).

Since neither the topography of the colony nor the behaviour of the birds can be standardized between colonies, these are irreducible constraints. The amount of observation, however, can be standardized to a certain extent. We recommend that plots containing about 80 sites be selected and observed for about 3 h daily. This should enable about 60% of eggs to be observed each day and about 50% of layings to be detected within 48 h. Thus, one observer could cover three plots comprising a total of 200–250 birds by working 9 h every day. This is quite close to the intensity of observation achieved in 1977, although in the Arctic weather conditions are almost certain to inhibit observations on some days.

## 2. Timing of breeding

### 2.1. Egg laying

In 1975, the first egg was recorded on the East Cliff colony on 20 June and eight eggs were present on an area supporting about 100 pairs on stack G3, half-way down the cliff, by 22 June; the first egg on a study plot was seen 23 June. In 1976 and 1977, first eggs were recorded on study plots on 20 and 21 June, respectively. Median laying dates for all plots combined were 28 June 1976 and 2 July 1977; in 1975 the median laying date for plot S1 only was 29 June compared with 3 July in 1976 and 1977 (Fig. 55).

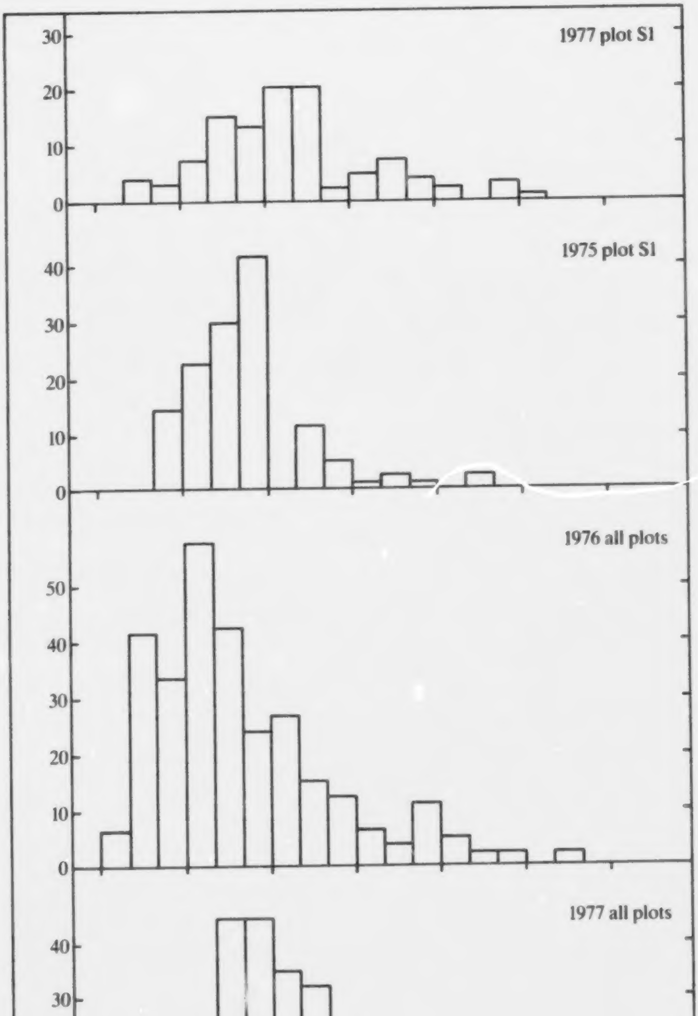
Although the timing of the earliest eggs was similar between years, the variance in laying dates differed considerably. On plot S1 in 1975, 83% of laying dates fell within the first 10 days of the laying period ($N = 128$). In 1976, 54% fell in the first 10 days, although definite laying dates were obtained for less than half the sites ($N = 79$); in 1977 only 40% of layings fell in the first 10 days ($N = 106$). Heterogeneity between years was significant ($\text{chi}^2 = 49.1$, df 2, $P < 0.001$). A possible explanation for the much greater synchrony of laying in 1975 than in the other two seasons lies in the temperature regime during the laying period. The mean temperature at 0700 h during the first 10 days of laying in 1975 was +4.5°C, compared with −0.8° and +0.7°C during the same periods in 1976 and 1977.

The latest laying of what we believed to be a first egg was on 17 July in 1975, 23 July in 1976, and 29 July in 1977, but the possibility that these were actually replacement eggs cannot be ruled out. The latest dates for all known layings were 28 July, 4 August, and 2 August, respectively. Appendices 10 and 11 give details of all laying dates known within 48 h for 1976 and 1977.

Comparison of laying dates between plots is complicated by large differences in the proportion of sites for which this datum was obtained accurately. A comparison of median laying dates between 1976 and 1977 suggests that these were totally uncorrelated (Spearman rank correlation coefficient, $r_s = 0.06$, $P > 0.5$), but a comparison of median hatching dates yields the opposite conclusion (see this chapter, section 2.2). There probably is a tendency for laying to be consistently earlier on some plots than on others. It would be surprising if this were not the case, since the laying dates at the same sites in different years were significantly correlated between years (Table 24).

The proportion of sites where eggs were relaid after the loss of the first egg was 29% ($N = 77$) in 1975, 31% ($N = 124$) in 1976, and 28% ($N = 93$) in 1977. These figures are inevitably underestimates because some first eggs would not have been detected before loss and what were actually second eggs were recorded as first eggs. Some relaid eggs must likewise have been lost before they were detected. Despite this drawback, the proportion of lost eggs that were replaced fell as the season progressed (Fig. 56). In 1977, for instance, the majority of eggs lost before 12 July were replaced, whereas pairs losing first eggs laid after 20 July did not relay. Assuming that the factors causing egg-loss are similar irrespective of date of laying, the

**Figure 55**
Distribution of laying dates observed within 48 h at all plots for 1976 and 1977 and at S1 for 1975 and 1977. Dates are combined into 2-day periods



chances of a replacement being laid are clearly higher when the first egg is laid early than when it is laid late.

The time elapsing between the disappearance of an egg and the laying of a replacement could be accurately measured only when the date of disappearance was known. In most cases birds that had lost an egg began to copulate immediately and this indicated that the egg was gone. The periods recorded ranged from 11 to 16 days ($N = 11$) in 1975, from 9 to 17 days ($N = 11$) in 1976 and from 11 to 17 days ($N = 20$) in 1977 (Fig. 57). Out of seven eggs removed experimentally from plot U on 5 July 1977, two were replaced in 13 days, one in 14 days, and four in 15 days. The plot was observed intensively during the

**Table 24**
Correlation coefficients for the dates of laying at the same site in different years*

| Study plot | 1975–76 | 1975–77 | 1976–77 |
|---|---|---|---|
| G | 0.84 (16)† | 0.29 (16) | 0.19 (21) |
| G4 | 0.67 (12)† | 0.41 (11) | 0.27 (18) |
| N | −0.56 (7) | 0.34 (3) | 0.98 (3) |
| Q1 | 0.43 (8) | 0.36 (6) | 0.19 (6) |
| Q4 | — | — | −0.60 (5) |
| S1 | 0.12 (59) | 0.28 (72)† | 0.32 (52)† |
| U | 0.40 (19)‡ | 0.20 (20) | 0.29 (34)† |

* Sample sizes are given in parentheses.
† $P < 0.01$.
‡ $P < 0.05$.

**Figure 56**
Proportion of eggs replaced in relation to the date on which the first egg was lost in 1977. Sample sizes refer to number of eggs for which date of loss was known

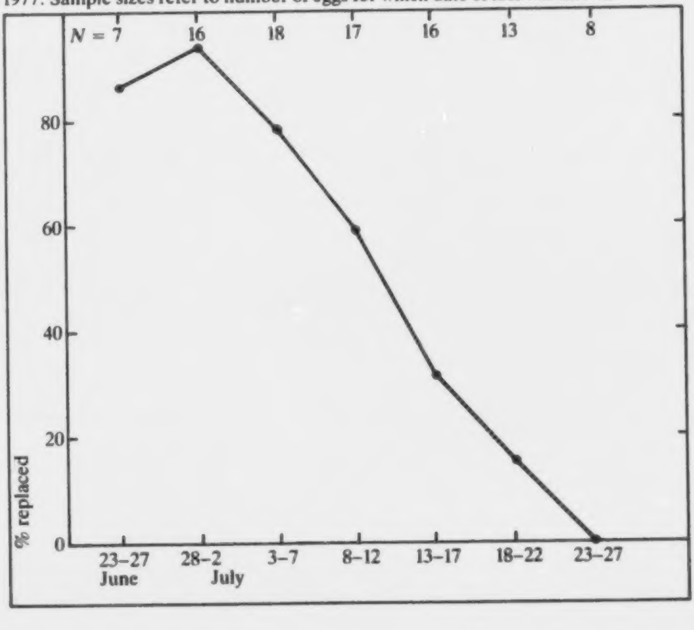
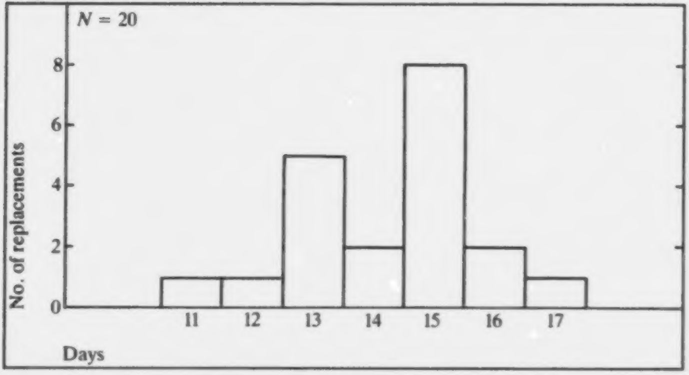


**Figure 57**
Length of time elapsing between the loss of an egg and the laying of a replacement, for periods known within 48 h in 1977



interim and records of replacement in as little as 9 days may have involved observational errors, although wide variation in replacement time has been observed for some seabirds [e.g., Northern Gannet, 6–32 days (Nelson 1966)].

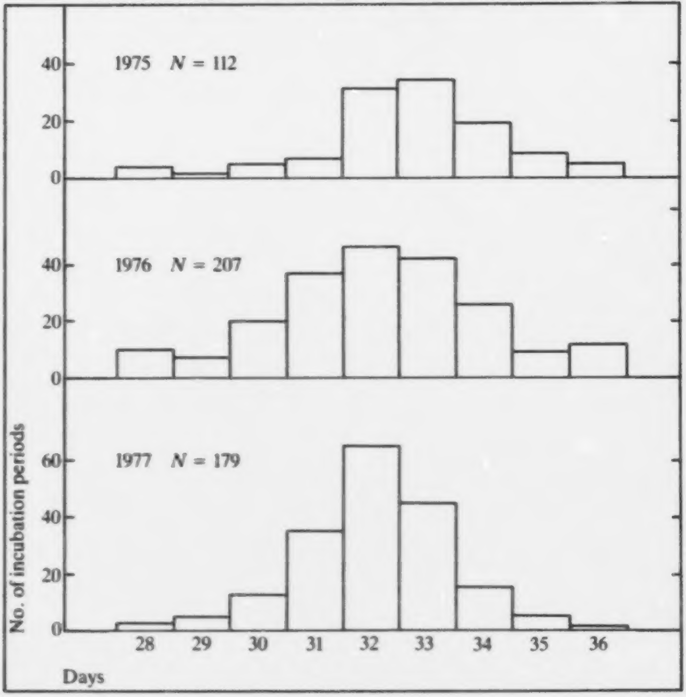
### 2.2. Hatching and length of incubation period

The length of the incubation period, calculated from dates of laying and hatching known within 48 h, varied from 28 to 36 days in 1975 ($N = 112$), from 25 to 40 days in 1976 ($N = 211$), and from 28 to 36 days in 1977 ($N = 179$). The median and modal lengths were 32 days in 1976 and 1977 and 33 days in 1975 (Fig. 58). Some of the extremes recorded may have involved errors. Since there is a maximum error of 4 days inherent in the calculation, variability is probably much lower than suggested by Figure 58 and nearly all eggs probably hatch between 31 and 34 days after laying, as found by Tuck (1961) at the Cape Hay colony. In calculating dates of laying from dates of hatching we assumed an incubation period of 32 days.

The first hatching was recorded on 24 July in 1975, on 20 July in 1976, and on 23 July in 1977. Although the date of hatching is closely tied to the date of laying, the progress of hatching is shown for all 3 years in Figure 59 because much larger samples were available for hatching than for laying (see also App. 12–14). The difference in the spread of laying dates between the three seasons is confirmed by the hatching dates, with 78% of hatching taking place in the first 10 days in 1975, 47% in 1976, and 30% in 1977 ($\text{chi}^2 = 210$, df 2, $P < 0.001$). Median hatching dates were 30 July in 1975 and 1976, and 3 August in 1977.

The timing of hatching in 1977 differed between plots (Fig. 60) and, although the heterogeneity was not significant within years, there was a significant tendency for the order of median hatching dates to remain constant from year to year (Table 25). Median hatching dates were earliest in all 3 years on plot G4 and latest on plot Q1. These differences do not relate either to aspect, or to hours of insolation, or

**Figure 58**
Lengths of incubation periods determined from laying and hatching dates known to within 48 h. (Incubation period of four eggs fell outside the range given in 1976)



to the timing of snow-melt. Date of hatching was related in a complex manner to certain characteristics of individual laying sites (see this chapter, section 4.3), but this did not account for the observed order of hatching either and the cause remains unknown. Observers had the subjective impression that pairs in certain parts of plots tended to lay earlier than others, but this was probably related to the type of site. Hatching dates for adjacent sites were not more synchronized than dates for the population as a whole (median difference in hatching dates between adjacent sites at S1 in 1977, 5.2 days; median for all pairs of sites on the plot, 4.7 days, $z = 0.99$, $P > 0.1$).

The tendency for the timing of breeding on particular sites to be correlated between years, already noted for laying dates, is more evident when the larger hatching samples are considered (Table 26), although no relationship seems to have existed on plot Q1. Many of the correlations are highly significant, but they explain relatively little of the total variation in hatching dates (up to 18%). The greater correlation between 1976 and 1977 than between either year and 1975 may be related to the highly synchronized laying which occurred in 1975.

The fact that sites explained only a small proportion of the inter-year variation in hatching dates may be because the bulk of the

**Figure 59**
Cumulative progress of hatching in three seasons expressed in 2-day periods. Due to incomplete data, plot Q4 is omitted for 1975

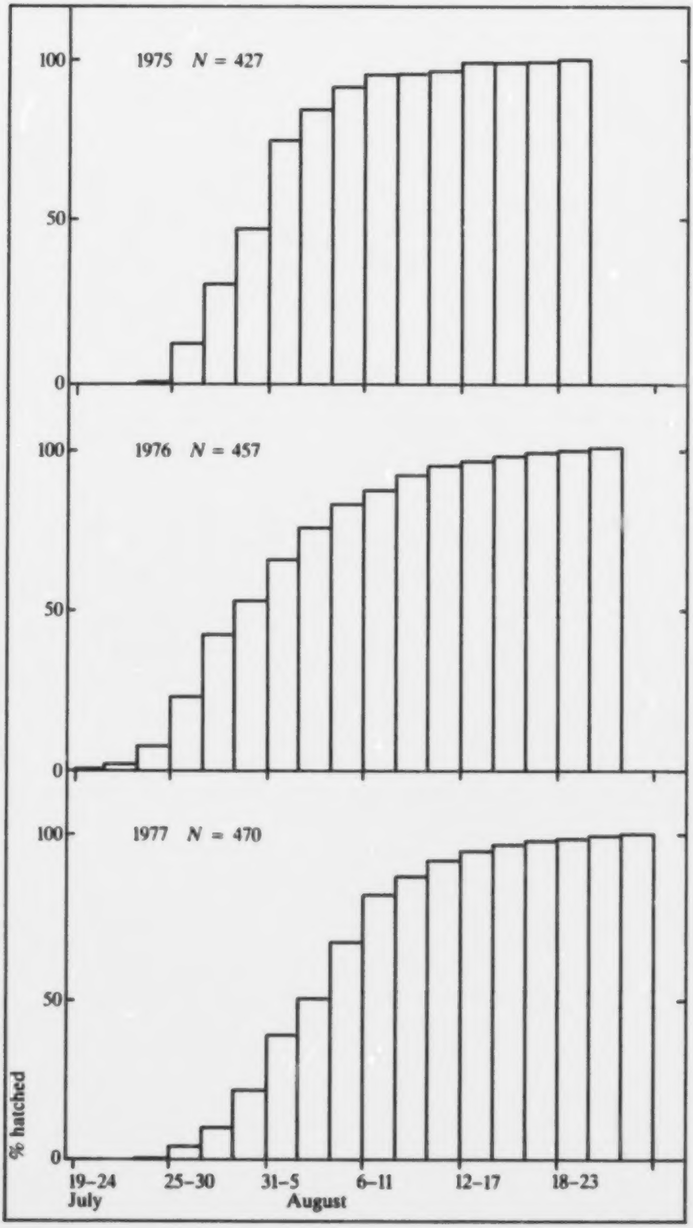
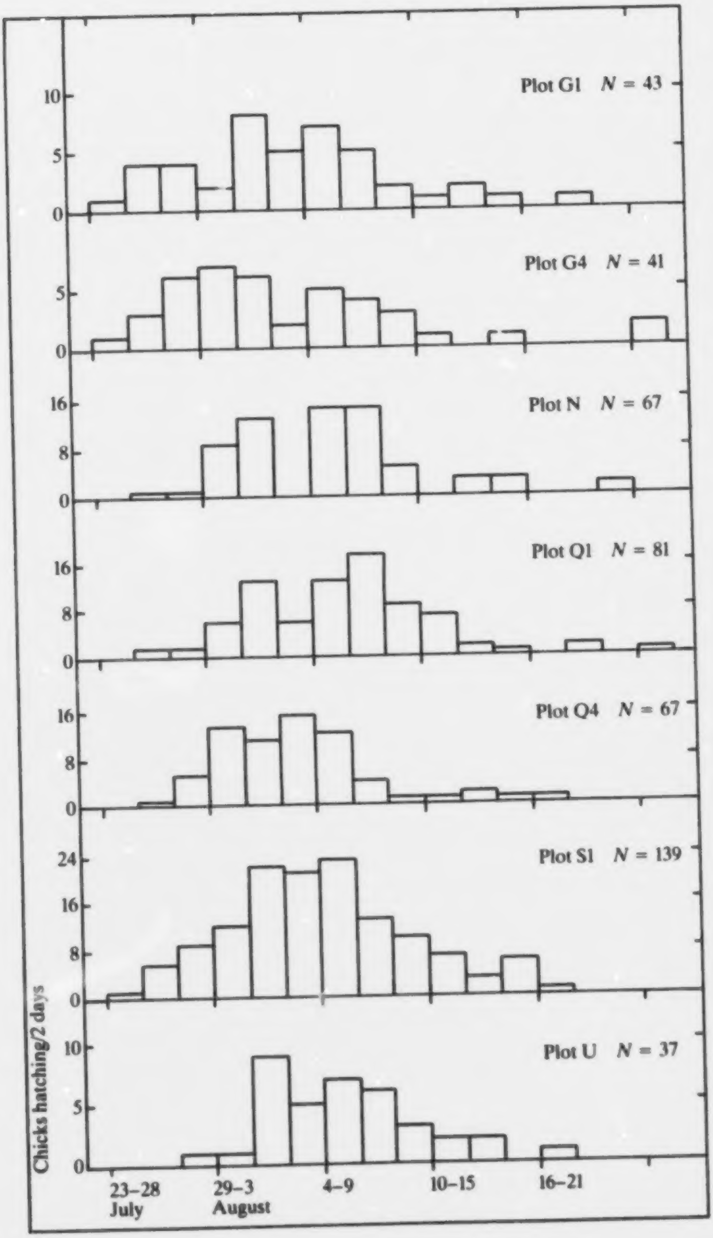


**Figure 60**
Number of chicks hatching per 2-day period on seven study plots in 1977



population laid at about the median date in each year. A more sensitive test of the tendency for eggs to be laid on particular sites at a similar date in relation to the rest of the population was obtained by analysing early-laying sites separately. At plot S1, where hatching dates were known in all three seasons for 76 sites, "early" chicks hatched during the first 4 days in 1975 (22.4%) and 1976 (18.8%) and the first 6 days in 1977 (16.0%). A comparison of the number of years in which sites produced early chicks with an expected frequency based on the null hypothesis that hatching dates in one year are independent of those in other years, showed that six times as many sites as expected had early chicks in every year (Table 27).

**Table 25**
Median dates of hatching at seven study plots in 1975, 1976, and 1977 (day 1 = 1 June)*

| Study plot | 1975 | 1976 | 1977 |
|---|---|---|---|
| G1 | 59.2 | 58.0 | 64.0 |
| G4 | 58.0 | 57.0 | 61.2 |
| N | 60.8 | 59.4 | 65.9 |
| Q1 | 61.7 | 63.5 | 66.0 |
| Q4 | 61.1 | 57.5 | 63.7 |
| S1 | 60.9 | 61.4 | 64.4 |
| U | 61.1 | 61.4 | 65.1 |

* Spearman rank correlation coefficients:
1975:1976 $r_s = 0.71$, $P \simeq 0.05$.
1975:1977 $r_s = 0.60$, $0.1 > P > 0.05$.
1976:1977 $r_s = 0.88$, $P < 0.02$.

**Table 26**
Correlation coefficients for the date of hatching at the same site in different years*

| Study plot | 1975–76 | 1975–77 | 1976–77 |
|---|---|---|---|
| G1 | 0.23 (30) | 0.16 (27) | 0.41 (36)* |
| G4 | 0.19 (24) | −0.05 (24) | 0.43 (28)† |
| N | 0.31 (55)† | 0.14 (42) | 0.18 (56) |
| Q1 | 0.07 (33) | 0.17 (59) | 0 (36) |
| Q4 | — | — | 0.03 (46) |
| S1 | 0.24 (99)‡ | 0.35 (98)† | 0.34 (107)* |
| U | 0.18 (33) | 0.24 (31) | 0.43 (28)† |

* Numbers in parentheses are sample sizes.
† $P < 0.01$.
‡ $P < 0.05$.

**Table 27**
Comparison of numbers of sites at plot S1 where chicks hatched early in 1, 2, or 3 seasons with expected frequencies based on the null hypothesis that dates of hatching at particular sites are independent between years. Only the 76 sites for which dates of hatching were known for all 3 years (1975–77) are included*

| | | No. of years in which hatching was early | | | |
|---|---|---|---|---|---|
| Frequencies | *N* | 0 | 1 | 2 | 3 |
| Observed | 76 | 45 | 13 | 11 | 7 |
| Expected | | 33.1 | 31.8 | 10.1 | 1.1 |

* $\text{Chi}^2 = 19.51$, df 2, $P < 0.001$ (lumping 2- and 3-year categories). Expected frequencies based on observed numbers of early sites: 1975 = 19, 1976 = 16, 1977 = 20.

### 2.3. Fledging and the duration of the chick-rearing period

The length of the chick-rearing period in the Thick-billed Murre was highly variable, ranging from 15 to 30 days, and was considerably modified in response to environmental factors. Observations of fledging behaviour indicate that the normal procedure involves an interaction between the chick and its parent and that a firm intention on the part of both is necessary for successful fledging (Chapter II, section 4.9). The possibility of a conflict of interest between the parent and the chick over the optimum length of the chick-rearing period cannot be ignored (Trivers 1974) and the process of resolving this conflict may contribute to the variability of the chick-rearing period. Other, probably more important, determinants include the nutritional state of the chick, presumably determined by the ability of its parents to provide food, and the weather and ice conditions at the colony during the fledging period.

The first fledgings from the study plots were observed on 12 August in 1975, 8 August in 1976, and 14 August in 1977. In 1975 observations terminated before the completion of fledging, but in 1976 the last chick fledged on 8 September and in 1977 on 11 September; therefore the duration of the fledging period (about 30 days, Fig. 61) was similar to that of the hatching period. The peak of fledging, however, was more concentrated than that of hatching. In 1976, 50% of hatching occurred within 8 days (26 July–2 August), whereas 50% of fledging took place over only 6 nights (17–22 August). In 1977, 50% of hatching took place in 7 days (30 July–5 August), but 50% of fledging occurred on 3 nights (20–21, 22–23, and 26–27 August). On the night of 22–23 August alone, 28% of all chicks reared on the study plots left the cliffs.

The number of chicks fledging was severely reduced by high winds (Fig. 61). Peak fledging occurred on still nights following periods of stormy conditions.

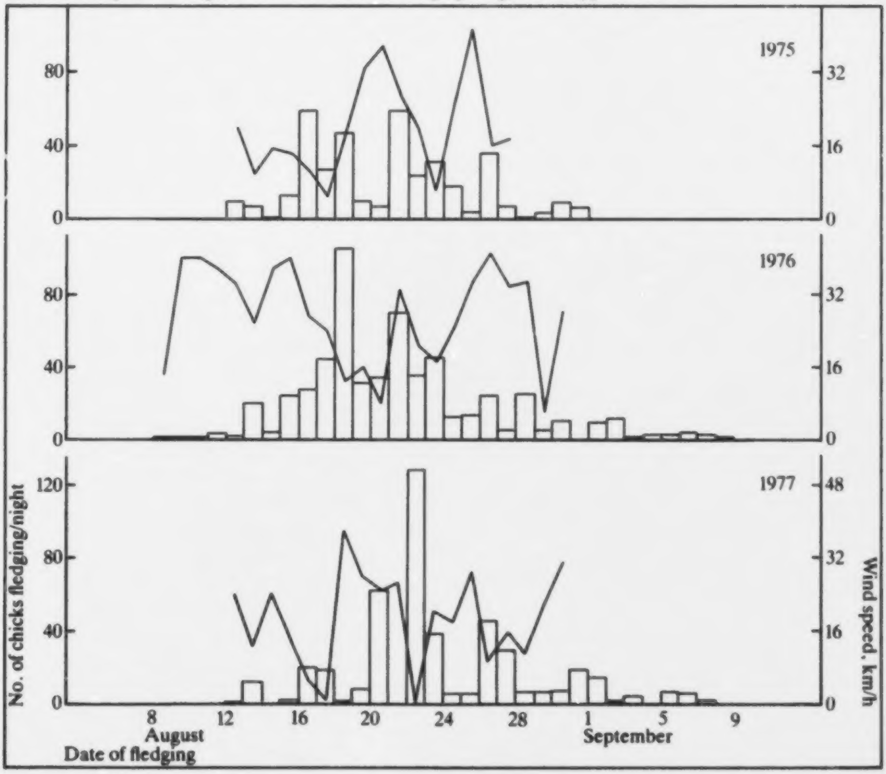
The mean duration of the chick-rearing period was 20.8 days in 1975 (based on plots G1, G4, N, S1, and U), 21.4 days in 1976, and 20.3 days in 1977. The variation about the mean was considerably greater in 1976 than in 1977 (Fig. 62), probably because of poorer weather conditions in 1976. The tendency for high winds to delay fledging is shown in Figure 63, which compares the age of chicks fledging on 16–17 August 1975, after a period of moderate winds (median age, 19.3 days) with those fledging on 21–22 August, after 2 days of winds over 32 km/h (median age, 21.3 days). A similar effect occurred in 1977 when the age of chicks fledging on 22–23 August (median age, 20.4 days), after 4 days of winds above 24 km/h, was higher than for those fledging the following night (median age, 18.9 days).

A negative correlation was found in all 3 years between the date of hatching and the duration of the chick-rearing period (Fig. 64). The effect was probably exaggerated in 1976 by strong winds which persisted throughout the early fledging period, up to 17 August, increasing the length of the chick-rearing period for the earliest cohorts. Evidence from 1975 and 1977 suggests that the trend is not important except for chicks hatching after 3 August, and hence involves only those chicks fledging during the second half of the fledging period. In fact, there is a suggestion in both 1975 and 1977 that the length of the chick-rearing period may increase initially with the date of hatching.

The length of chick rearing for replacement eggs was similar to that of first eggs hatching at the same date (Fig. 64).

There are several reasons why chicks that hatch after the median date for the population fledge at a younger-than-average age. Firstly, it enables them to fledge closer to the peak for the colony and hence to take advantage of the swamping effect on Glaucous Gull predation. Secondly, ice conditions in Lancaster Sound deteriorate rapidly after the end of August and it must take the chicks a minimum of 2–3 weeks to travel to Baffin Bay, judging from the surveys of Johnson *et al.* (1976). For the adult birds, which begin to moult soon after leaving the colony, it is also important to get away from the colony rapidly because they become flightless at that time (Birkhead and Taylor 1977). If late-hatching chicks have a lower probability of survival after fledging than early chicks, then, paradoxically, their parents are likely to be less solicitous, as the chicks represent a lower potential benefit in terms of reproductive success, and hence do not warrant a large investment of energy or any lowering of potential

**Figure 61**
Numbers of chicks fledging each day in 1975, 1976, and 1977. Each bar represents the number of chicks which had departed during the previous night. The solid line gives the mean of the wind speed at 0700 h and at 1900 h the previous night. Details of numbers fledging are given in Appendices 15–17



survival on the part of their parents. Chicks, therefore, may have to fledge before they reach optimum physical condition, partly to adjust to the interests of their parents.

### 2.4. Factors influencing timing of breeding

The timing of breeding in the three seasons of the study (1975–77) was very similar. Despite the fact that conditions differed considerably between seasons, median laying dates fell within 5 days, dates of first eggs within 4 days, and the total spread of laying lasted 35–45 days. In 1976 the nearest major ice edge to the colony during the pre-laying period was 120 km away across the south end of Wellington Channel, whereas in the other 2 years there was fast ice adjacent to the island. Land-fast ice edges are very important feeding areas for murres during the pre-laying period (Bradstreet 1977) and many birds, presumably from Prince Leopold Island, were present at the Wellington Channel ice edge during June 1976, and also at the edge of fast ice between Griffith and Cornwallis islands, about 180 km

**Figure 62**
Age at fledging of chicks at all plots in 1976 and 1977, calculated from hatching and fledging dates known within 48 h and 24 h, respectively. The shaded bar for 1977 gives the ages of chicks actually seen fledging. Comparing means between 1976, 1977, $t = 5.85$, $P < 0.001$. Comparing variances, $F = 1.93$, $P < 0.01$

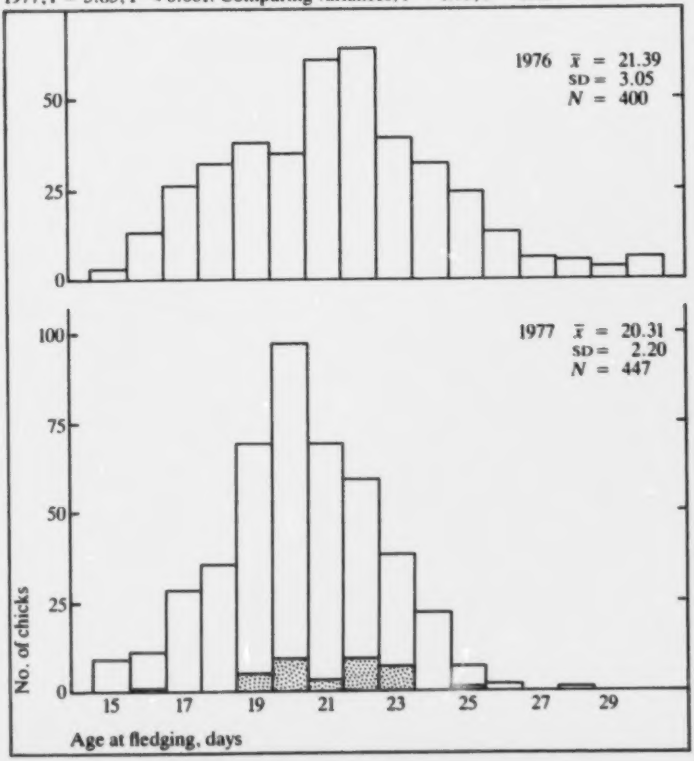


**Figure 63**
Comparison of the ages of chicks fledging after a period of moderate winds with those fledging after 2 days of high winds; Mann-Whitney $U = 2097$, $Z = 5.3$, $P < 0.001$

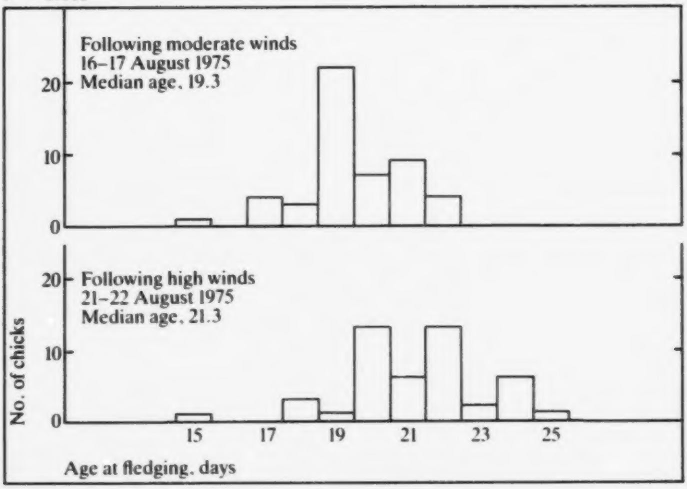
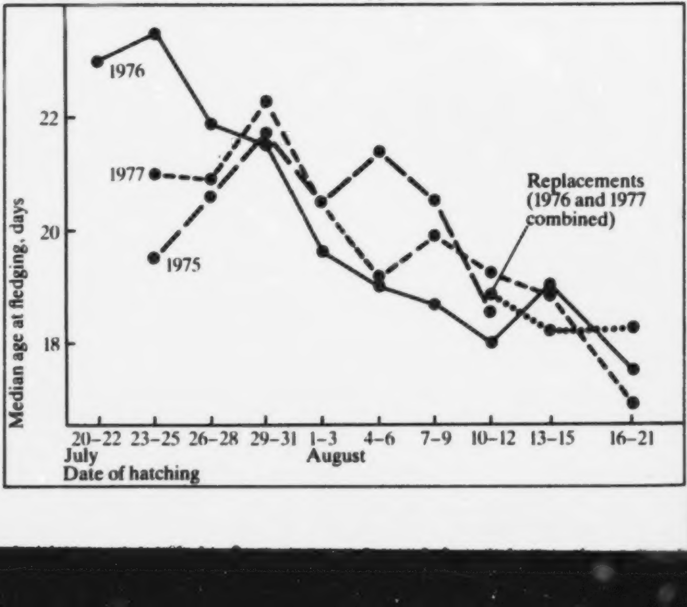


**Figure 64**
Age at fledging in relation to the date of hatching for all 3 years, 1975–77. Rank correlation coefficients: 1975, $r_s = -0.79$, $P < 0.05$; 1976, $r_s = -0.95$, $P < 0.01$; 1977, $r_s = -0.90$, $P < 0.01$. Data from Appendices 18–20



from the colony. With feeding areas so far from the colony, we might have predicted that laying would be retarded in 1976, but this was not so and laying was slightly earlier in 1976 than in the other 2 years.

Timing of breeding in birds is controlled partly by extrinsic factors, such as the food supply (Marshall 1951, Perrins 1970, Jones and Ward 1976) and partly by an intrinsic rhythm, in most cases entrained by photoperiod (Thomson 1950; Marshall 1959; Farner 1964, 1967; Murton and Westwood 1977). In general, development of the sex organs is dependent on the internal rhythm, while the actual development of the egg is controlled by events in the external environment, although these two systems certainly interact. In species for which optimum conditions for breeding develop over a short period of time, birds laying early have better breeding success than late layers. It has been suggested that in such cases the timing of laying is determined by the ability of the female to develop the eggs (Perrins 1965) or to maintain itself during incubation (Brooke 1978). In other cases, females may be capable of forming eggs for some time prior to laying, but delay in response to one or more environmental cues, presumably timed so that the young are being reared when suitable food is most abundant (Lack 1968). For these species, birds laying during the peak of laying are more successful than those laying early or late. In either case part of the variance in laying dates may be determined by differences in the strategies adopted by individual birds, perhaps based on genetic variability within the population (Bryant 1979).

Belopol'skii (1957) has suggested that the availability of food during the pre-laying period is crucial in determining the date of laying in murres. Dates of first laying observed in Novaya Zemlya over nine seasons, however, all fell within a period of 5 days, which suggests that timing was determined by some cue which varied little from year to year (Uspenski 1956). A similar conclusion can be drawn from the uniformity of laying dates observed at Prince Leopold Island, where there were big differences in the distances of preferred feeding areas between seasons. It is difficult to believe that food supplies would be sufficiently predictable from year to year. The observed decline in breeding success with date of laying (see this chapter, section 3.3), on the other hand, suggests that birds laying at the end of the season may have been prevented from doing so earlier by their inability to form eggs.

To explain most of the observed features of timing of breeding we assume that in some years part of the population is capable of laying some days before it actually does so and "holds back" to optimize the timing of chick rearing, while the rest of the population is not capable of laying at the optimum time, due to energy constraints. This hypothesis predicts that the relationship between the date of laying and breeding success should be most marked when most of the population is not in a position to lay at the optimum time, and this may have been the case in 1976, which combined an early season (in terms of ice break-up) with possible difficulties in feeding during the immediate pre-laying period. The opposite situation arose in 1977 when, in an apparently late season, the effect of laying date on breeding success was relatively small (see Chapter II).

The distribution of laying and hatching dates in all three seasons was skewed to the right, with a rapid increase in laying at the start of the season and a more gradual decrease after the modal date. This distribution fits the prediction that some birds are timing their laying to some phenomenon other than their state of nutrition, rather than laying as soon as they are capable. A delay of this sort could confer the following benefits on the birds involved:

(1) hatching is timed to coincide with the peak abundance of suitable food for the chick,

(2) the time during which the egg is exposed to predation without the benefit of incubating neighbours is reduced, and

(3) the chick is able to fledge at the peak period without an abnormal extension of the chick-rearing period.

All of these factors may be involved, although there is no evidence to support the first. Bad weather just after the start of laying causes the majority of birds that are not already incubating to leave the colony, leaving those birds which do have eggs relatively unprotected, and hence vulnerable to predation by gulls (Chapter II, section 4.10). At fledging, chicks that hatch early are faced with the choice of prolonging their stay on the cliffs, with the attendant risks of predation or rock-falls, or fledging before the majority and running a higher risk of predation at that stage.

Timing of laying at Prince Leopold Island is very similar to that at the large Thick-billed Murre colony near Cape Hay, Bylot Island, 300 km to the east. In 1957 Tuck (1961) recorded the first egg on 20 June and the laying period was of similar duration to that recorded at Prince Leopold Island. In 1976 Cape Hay was visited on 13 August and the age of most of the chicks was similar to the ages of chicks at Prince Leopold Island in the same year (Gaston and Nettleship unpubl.). Since the fast ice always clears from the vicinity of Cape Hay before it clears farther west, this provides further evidence that the breeding of murres in the Lancaster Sound area is timed to coincide with certain events in the marine environment, events which are presumably similar at Cape Hay and Prince Leopold Island, rather than taking place as soon as the birds are capable of forming eggs.

Despite the apparently very short season available for breeding, between the breakup of the ice and the arrival of snowstorms in September, the spread of laying dates for the Thick-billed Murre at Prince Leopold Island was very similar to that for several temperate alcids, such as the Common Murre (Birkhead 1976*a*, 1977*a*), Atlantic Puffin (Nettleship 1972, Ashcroft 1976) and Razorbill (Lloyd 1976). The proportion of lost eggs that was replaced was smaller than that for the Thick-billed Murre at other arctic colonies (Tuck 1961, Belopol'skii 1957), but in these instances the colonies studied were heavily disturbed and egg loss may, therefore, have occurred earlier than usual. This may also account for the laying of second replacement eggs after the loss of the first replacement, which was not observed at Prince Leopold Island. The duration of the replacement period is such that second replacements can only occur if two successive eggs are lost immediately after laying and this seems unlikely, particularly for eggs laid early in the season in an undisturbed situation. Belopol'skii (1957) also considered the laying of two replacements unlikely under natural conditions. The length of the period between loss and replacement observed at Prince Leopold Island was similar to that recorded by Tuck (1961) and also to that found for the Common Murre on Skomer

Island, Wales, by Birkhead and Hudson (1977). Since the period apparently varies little with latitude, the maximum rate of development of the egg may be fixed by physiological constraints common to the two species of *Uria*.

If the energy budget of the female prior to laying affects the development of the egg, then the difference in temperature between the top and the bottom of the cliffs at Prince Leopold Island (probably about 2°C, according to the normal declination of temperature with altitude) should affect the timing of laying. This is supported by the earlier laying observed in 1975 on stack G3, halfway down the cliff. The difference is equivalent to many degrees of latitude for birds breeding at the same height. An inverse correlation between date of laying and spring temperatures has been demonstrated by Hedgren (1979) for Common Murres in the Baltic Sea. There may also be a trade-off between the date of laying and the size of the egg, since females may in some cases be faced with the choice of laying a relatively small egg or returning to feed again and producing a larger one at a later date (see Chapter IV).

Thick-billed Murres incubating eggs or brooding young chicks (D.N. Nettleship)

## 3. Breeding performance

### 3.1. Hatching success

Although attempts were made in 1975 and 1976 to monitor breeding success at 11 plots, only the 7 plots studied in 1977 are included in the following analysis of the 3 years. Overall hatching success of first eggs was estimated at 84% in 1975, 75.7% in 1976, and 78.1% in 1977 (Table 28). The number of eggs recorded on the seven plots was lower in 1975 (626) than in 1976 and 1977 (659, 650), but the total numbers of birds present during daily counts was similar. At the plots observed most intensively in 1975 (G1, S1, U), the number of eggs recorded was slightly higher in 1975 than in 1976 (300 vs. 295) and the less intensive observations made in 1975 possibly resulted in a higher proportion of eggs being overlooked, biasing the estimated hatching success upwards (see this chapter, section 1.1). If we assume that the actual number of eggs laid in 1975 was the same as in 1976, then hatching success can be estimated as 79.8%, close to the level observed in 1977. If, in addition, plot Q1, which suffered heavy snow accumulation during the incubation period in 1976, is excluded from that year's figures, then hatching success for 1976 can be estimated at 80.0% (*N* = 550). With these two corrections, hatching success for all three seasons falls between 78 and 80% for first eggs.

We do not know the cause of disappearance of most eggs, but we did observe some egg mortality on plot S1 in 1975 and 1977 (Table 29). We assumed that some eggs, which remained unhatched beyond the normal incubation period, were infertile or became chilled and/or addled at some stage during incubation. These constituted 3.6% of all eggs reaching at least 35 days in 1975, 5.5% in 1976, and 7.5% in 1977.

The rate of disappearance of eggs was highest immediately after laying and fell throughout the incubation period (Fig. 65). Between 11 and 35 days, during which period the rate of loss changed only slightly, the mean rate was 0.30% per day (*N* = 584) in 1977. A few eggs recorded as lost between 30 and 35 days may actually have hatched and the chick disappeared immediately.

The hatching success of first eggs declined with date of laying in all 3 years, although only plot S1 could be analysed in 1975. The effect was more marked in 1976, when hatching success fell from 82.6% for eggs laid during 20–24 June to 60.0% for eggs laid on 10 July or later,

**Table 28**
Numbers of eggs laid, hatched, and fledged on seven study plots in 1975–77

| Year | First eggs* | | | Relays* | | | Breeding success, % (total fledged/total first eggs) |
|---|---|---|---|---|---|---|---|
| | Laid | Hatched | Fledged | Laid | Hatched | Fledged | |
| 1975 | 626 | 526 (84.0) | 486 (92.4) | 22 | 18 (81.8) | 7 (38.9) | 78.8 |
| 1976 | 659 | 499 (75.7) | 436 (87.4) | 39 | 23 (59.0) | 15 (65.2) | 68.4 |
| 1977 | 643† | 502 (78.1) | 470 (93.6) | 26 | 19 (73.1) | 16 (84.2) | 75.6 |

*Figures in parentheses are percentages.
†Excludes seven eggs experimentally removed from plot U to induce relaying.

than in 1977 (Fig. 66) and the difference was similar when the anomalous plot Q1 was excluded. In both cases the decline was most marked after the date by which 80% of the eggs had been laid. The proportion of eggs that were incubated to full term but failed to hatch did not show any relationship with date of laying, varying in 1977 between 5.4 and 9.3% for different cohorts.

**Table 29**
Causes of egg mortality observed at study plot S1 in 1975 and 1977 (data not recorded in 1976)

| Cause of egg mortality | 1975 | 1977 |
|---|---|---|
| Gull predation | 5 | 0 |
| Slipped off after being laid on snow | 0 | 3 |
| Rolled off ledge | 1 | 2 |
| Wedged in crack | 4 | 2 |
| Crushed | 1 | 0 |
| Dislodged during intraspecific fighting | 0 | 1 |
| Dislodged when incubating parent was buffeted by high winds | 0 | 1 |
| Did not hatch by day 36 | 8 | 13* |

* Includes two eggs laid on snow.

**Figure 65**
Rates of loss of eggs and chicks (in 1977) in relation to the time elapsing since laying (lower scale) and hatching (upper scale). Both horizontal axes are plotted on a $\log_{10}$ scale. Rates of loss are calculated as percentages of the number of eggs/chicks available at the start of the period. Thirteen eggs for which the timing of loss was not known were assigned proportionately to the six periods

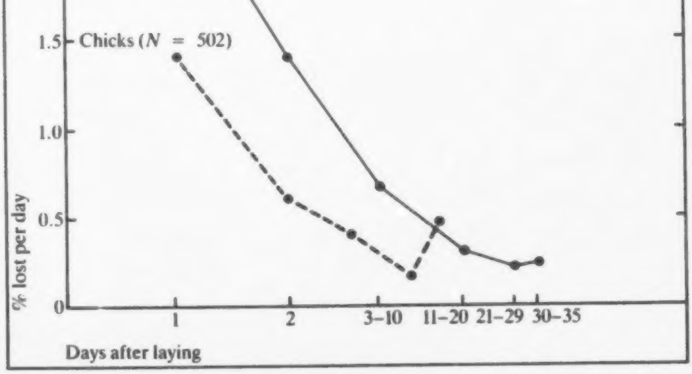


**Figure 66**
Hatching success in relation to date of laying in 1976 and 1977. Dates are combined into 5-day periods

| | N | | | | |
|---|---|---|---|---|---|
| 1977 | 15 | 67 | 74 | 54 | 41 |
| 1976 (excl.Q1) | 57 | 98 | 49 | 18 | 16 |
| 1976 (incl.Q1) | 64 | 115 | 60 | 23 | 16 |

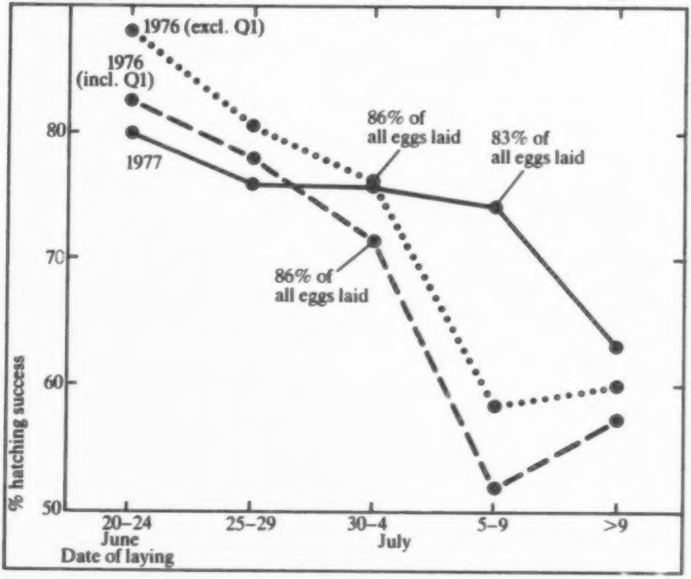
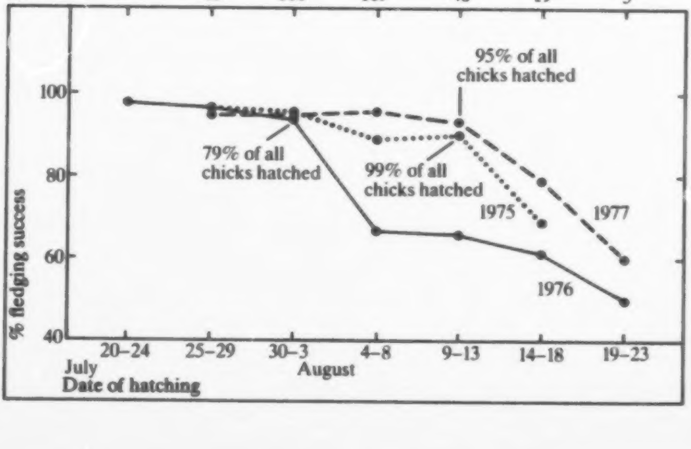


**Figure 67**
Fledging success in relation to the date of hatching in all 3 years, 1975–77. Values for 1975 exclude Q4, those for 1976 include plots S3 and M

| | N | | | | | | |
|---|---|---|---|---|---|---|---|
| 1975 | — | 139 | 125 | 33 | 15 | 3 | — |
| 1976 | 57 | 217 | 202 | 70 | 35 | 13 | 10 |
| 1977 | — | 65 | 166 | 169 | 48 | 19 | 5 |



### 3.2. Fledging success

Figures for fledging success should be similarly reliable for all 3 years and estimates of 92.4, 87.4, and 93.6% were obtained for chicks hatched from first eggs (Table 28), which suggests a fairly constant fledging success of about 90% of chicks that hatch. Causes of chick mortality observed included falling off the ledge, becoming wedged in a crack, and predation by Glaucous Gulls. Mortality was highest immediately after hatching (Fig. 65), falling to less than 0.2% per day between 7 and 10 days after hatching and then rising between 11 and 14 days, perhaps because a few chicks attempted to fledge at this age (see this chapter, section 1.1).

Fledging success, like hatching success, declined as the season progressed (Fig. 67), although the effect was most marked in 1976, particularly for the last 20% of chicks to hatch. In 1977 the decline was apparent only for chicks hatched after 14 August and the high survival of earlier cohorts probably reflects a greater availability of food for the chicks in this season (see Chapter IV, section 3). The fledging success of replacements was 65.2% in 1976 ($N = 23$) and 84.2% in 1977 ($N = 19$), similar to that of first eggs hatched at the same time, but the fledging success of replacements in 1975 was lower (38.9%, $N = 18$) and there was significant heterogeneity between years (chi$^2$ = 8.28, df 2, $P < 0.02$).

### 3.3. Breeding success

The overall breeding success, calculated from the total number of chicks fledged, including replacements, in relation to the number of first eggs laid, was estimated as 78.8% in 1975, 68.4% in 1976, and 75.6% in 1977 (Table 28). Assuming the number of eggs laid in 1975 was the same as in 1976, the breeding success in 1975 is estimated at 74.8% and for all 3 years between 68 and 76%.

The success of first eggs was 77.6, 66.2, and 73.1% in the three seasons, with the proportion of lost eggs that were replaced remaining fairly constant at 22.0, 24.4, and 18.4% respectively. However, the success of replacements was higher in 1977 than in the other two seasons (chi$^2$ = 4.97, df 2, $0.1 > P > 0.05$), which increases overall breeding success relative to 1975 and 1976.

The proportion of lost eggs that were replaced declined as the season progressed and hence the proportion replaced was inversely related to the date of laying (Table 30). This effect tended to increase the difference in breeding success between early and late layers (Fig. 68), although the difference was relatively small in 1977 for eggs laid up until 9 July (84% of first eggs) and in 1976 for eggs laid up until 4 July (83% of first eggs). If the 100% success of the small sample for

**Table 30**
Proportion of lost eggs that were replaced in relation to the date of laying of the first egg*

| Year | ≤ 30 June | 1–6 July | ≥ 7 July |
|---|---|---|---|
| 1975† | 50% (12) | 31% (13) | 0% (3) |
| 1976 | 82% (17) | 50% (20) | 17% (18) |
| 1977 | 46% (13) | 43% (23) | 0% (19) |

* Sample sizes in parentheses.
† Values for 1975 from study plot S1 only.

**Figure 68**
Breeding success in relation to date of laying in all 3 years, 1975–77. Figures for 1975 are for S1 only

| | *N* | | | | |
|---|---|---|---|---|---|
| 1975 | 7 | 57 | 44 | 12 | — |
| 1976 | 62 | 116 | 60 | 23 | 26 |
| 1977 | 15 | 68 | 88 | 55 | 42 |

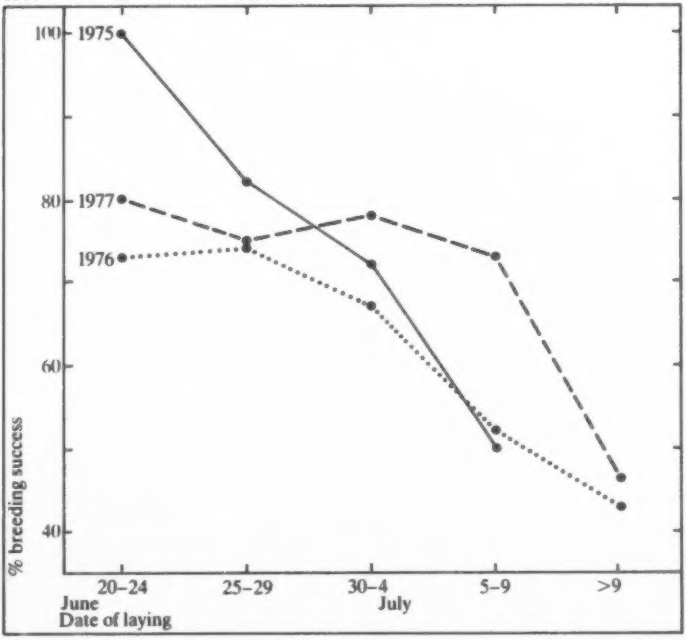


**Table 31**
Hatching, fledging, and breeding success (%) at seven study plots in 1975–77

| Study plot | Hatching success | | | Fledging success | | | Breeding success | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1975 | 1976 | 1977 | 1975 | 1976 | 1977 | 1975 | 1976 | 1977 |
| G1 | 90.7 (54) | 85.2 (54) | 86.8 (53) | 95.9 | 95.7 | 97.8 | 88.9 | 83.3 | 88.7 |
| G4 | 75.9 (58) | 70.3 (64) | 62.7 (67) | 97.7 | 88.9 | 85.7 | 74.1 | 62.5 | 55.2 |
| N | 87.7 (81) | 85.1 (101) | 84.4 (96) | 94.4 | 89.5 | 95.1 | 85.2 | 77.2 | 80.2 |
| Q1 | 86.1 (101) | 54.1 (109) | 77.0 (109) | 85.1 | 69.5 | 91.7 | 73.3 | 40.4 | 71.6 |
| Q4 | 82.6 (86) | 83.3 (90) | 77.0 (87) | 93.0 | 80.0 | 94.0 | 76.7 | 67.7 | 77.0 |
| S1 | 79.2 (178) | 79.5 (176) | 80.4 (179) | 95.0 | 92.9 | 95.8 | 77.0 | 78.4 | 77.1 |
| U | 92.6 (68) | 73.8 (65) | 73.1 (52)* | 87.3 | 91.7 | 89.5 | 82.4 | 70.8 | 69.2 |
| $\bar{x}$ | 85.0 | 75.9 | 77.3 | 92.6 | 86.3 | 92.8 | 79.7 | 68.6 | 74.1 |

Spearman rank correlation coefficients ($r_s$) and Kendall coefficient of concordance (*W*):

| | 1975–76 | 1975–77 | 1976–77 | *W* |
|---|---|---|---|---|
| Hatching success | 0.36 | 0.36 | 0.71 | 0.65† |
| Fledging success | 0.54 | 0.21 | 0.61 | 0.63† |
| Breeding success | 0.88† | 0.68 | 0.87† | 0.87‡ |

Correlation of hatching and fledging success:

| 1975 | 1976 | 1977 |
|---|---|---|
| −0.43 | 0.61 | 0.93‡ |

* Excludes seven eggs removed experimentally. † $P < 0.05$. ‡ $P < 0.01$.

**Table 32**
Comparisons of breeding success at the same site in different years*

| | 1976 | | | |
|---|---|---|---|---|
| | Successful | Unsuccessful | Chi$^2$ | $P$ |
| 1975 | | | | |
| Successful | 324 | 127 | | |
| Unsuccessful | 64 | 39 | 3.92 | $\simeq 0.05$ |
| | 1977 | | | |
| | Successful | Unsuccessful | | |
| 1975 | | | | |
| Successful | 347 | 99 | | |
| Unsuccessful | 66 | 32 | 4.81 | $<0.05$ |
| | 1977 | | | |
| | Successful | Unsuccessful | | |
| 1976 | | | | |
| Successful | 337 | 83 | | |
| Unsuccessful | 105 | 59 | 16.67 | $<0.01$ |

| | 1975 | 1976 | |
|---|---|---|---|
| | | Successful | Unsuccessful |
| 1977 Successful | Successful | 257 (236.2) | 77 (88.7) |
| | Unsuccessful | 52 (52.2) | 11 (27.6) |
| 1977 Unsuccessful | Successful | 60 (73.4) | 32 (23.9) |
| | Unsuccessful | 9 (16.2) | 22 (5.3) |

* Expected frequencies are given in parentheses:
Chi$^2$ = 74.4, df 7, $P < 0.01$.

20–24 June 1975 is ignored, breeding success for the majority of eggs in all three seasons is fairly uniform, declining sharply after ca. 80–85% of the population has laid. As the hatching and fledging success of replacement eggs is similar to that of first eggs laid at the same date, the observed decline in breeding success for late eggs is probably due mainly to deterioration in the environment, rather than the result of inexperienced or poor quality birds laying late in the season.

Relative hatching, fledging, and breeding success was similar among plots from year to year, the similarities being greatest between 1976 and 1977 (Table 31). Considering success at individual sites in all 3 years, there was a highly significant tendency for the same sites to fail. Four times as many sites failed in all 3 years as the number predicted by the hypothesis that breeding success in one year was independent of success in other years (Table 32).

Because the study plots contained unequal numbers of birds, estimates of reproductive success based on combined totals might be biased. However, estimates of hatching, fledging, and breeding success calculated as the means of individual plots are very close to those derived from the combined data (Tables 28 and 31). The largest plot, S1, ranked about midway in breeding success in all 3 years.

Two birds were observed at a number of sites from which chicks had fledged, and these couples sometimes copulated or allopreened, suggesting that they were the members of the original pair. L.M. Tuck (pers. commun.) also found that two marked birds present at a site after the chick had fledged were the original pair. Where this occurred, we assumed that the chick had probably died; Lloyd (1976) made this same assumption for Razorbills. In many cases we could not be sure to which site these pairs belonged as they were together for only short periods, preventing us from making a reasonable estimate of immediate post-fledging mortality. At plot S1, however, where several 24-h watches were carried out in the second half of August, a minimum of 25% of sites appeared to have lost their chick within a few days of fledging in 1975 and a minimum of 30% in 1977 (these data were not recorded in 1976). This indicates a mortality equal to that during the entire incubation and chick-rearing periods, although mortality at time of fledging may be considerably higher at plot S1 than elsewhere in the colony due to the physical structure of the cliffs at this location, which makes it difficult for chicks to reach the sea accompanied by their parents.

### 3.4. Inter-plot comparisons

Differences in breeding success among the seven plots studied intensively in all 3 years were similar from year to year (Table 31). Hatching success was positively correlated among all three combinations of seasons, but the correlation was best between 1976 and 1977, perhaps because records of egg laying were less accurate in 1975 than in the other two seasons.

Rankings of plots for breeding success were closely correlated between seasons, with plot G1 being the most successful in all 3 years and plots G4 and Q1 sharing the lowest two ranks. The timing of laying on each plot could be compared only for 1976 and 1977 and no correlation was found among median laying dates ($r_s = 0.14$, $P > 0.5$). Median dates of hatching were positively correlated among all seasons (Table 25), but were not correlated with breeding success; and although breeding success was positively correlated with median laying date in 1976, it was not in 1977. Most of the difference between the two seasons was due to plot G4, which ranked sixth in laying date in 1976, but first in 1977, although it ranked sixth in breeding success in both years. The observed difference may have been due to circumstances peculiar to plot G4, perhaps local weather effects.

An *a priori* classification of plots into those considered peripheral (G1, Q1 — both at the top of the cliff and spread over well-spaced ledges) and those considered central (G4, Q4 — below the cliff-top with breeding ledges packed close together) was not related to breeding success, nor was the aspect that the plot faced, since plots G1 and G4 and Q1 and Q4 were on the same cliff faces and had the same exposure but showed very different breeding success (Table 31). The differences in breeding success observed between plots probably cannot be attributed to any difference in general features of the plots, but rather are determined by the relative suitability of their constituent breeding sites (see this chapter, section 4.2).

# 4. Factors affecting breeding success

## 4.1. Persistence of site occupancy from year to year

Relatively little information was obtained on the site-tenacity of individual birds. Four birds were individually colour-banded in 1975, another four in 1976, and six in 1977. The birds in the 1975 sample were all on, or within 1–5 cm of, the same sites in 1976 and at least three were present in 1977. Three of the 1976 sample occupied the same sites in 1977, and the fourth was seen sporadically on a site about 3 m away from its original location, although it did not breed. This bird was not seen until late July and hence may have attempted to breed on its original site and failed. All six birds marked in 1977 were on the same sites in 1978. Therefore, birds generally use the same sites from year to year and in most cases where sites are occupied in successive years the same pair is presumably involved. Similar site-tenacity has been observed in the Common Murre (Southern *et al.* 1965, Birkhead 1977*a*) and other alcids (Nettleship 1972, Lloyd 1976).

Out of 652 sites occupied on the study plots in 1976, 10.1% were not used in 1977, while 8.9% of the sites occupied in 1977 had not been used in the previous year (comparisons with 1975 have been ignored because of the possibility that some sites were misidentified during renumbering in 1976). Some of these changes of site must have involved birds that had bred in 1976 and relocated in 1977 and some birds breeding for the first time. Some of the disappearances may be due to mortality during the non-breeding season. Changes of site were dictated in some cases by changes in the structure of the breeding ledges. Between 1976 and 1977 a ledge supporting one site on plot U, another supporting three sites on G1, and a third with two sites on G4 disappeared as a result of erosion. These six sites are < 1% of the total sites, but if the six pairs involved relocated on new sites on the same plots they represented 10% of the birds occupying new sites. In 1975 a large rock-fall struck plot Q4 during the pre-laying period and destroyed some ledges that were occupied. Rock falls must also create new sites and, where several are formed close together as a result of the same fall, they may be colonized by young birds, creating a group of similar age which may persist for a considerable time.

Of sites occupied in 1976 but not in 1977, 34.8% succeeded in fledging chicks from first eggs, compared with 69.5% of sites occupied in both years. The success in 1977 of sites not occupied in the previous year was 59.6%, compared with 74.4% for those occupied in both. These differences appeared to be consistent for all plots (Table 33). Altogether, 17.5% of sites which were unsuccessful in 1976 were not occupied in 1977, compared with 5.3% of successful sites (Table 34). If sites not occupied in 1975 are considered separately, then the effect is greater, with 47.1% of sites that failed being unoccupied in 1977, compared with 8.9% of successful sites. The effect for sites occupied in 1975 and 1976 is smaller, though still significant, with 12.8% of unsuccessful sites being unoccupied in 1977, against 4.9% of successful sites.

Comparing hatching dates, the proportion of eggs laid on sites that had not been used in the previous year rose as the season pro-

**Table 33**

Success of first eggs at sites not occupied in either of 1976 and 1977, compared with success at sites occupied in both years[*]

| | % of first eggs from which chicks fledged ($N$) | | | |
|---|---|---|---|---|
| | | | Success at sites occupied in both years | |
| Study plot | Success in 1976 of sites not used in 1977 | Success in 1977 of sites not used in 1976 | 1976 | 1977 |
| G1 | 50 (4) | 67 (3) | 84 (50) | 86 |
| G4 | 50 (8) | 36 (11) | 64 (56) | 57 |
| N | 33 (12) | 71 (7) | 82 (89) | 81 |
| Q1 | 8 (13) | 61 (13) | 42 (96) | 72 |
| Q4 | 33 (6) | 33 (3) | 69 (84) | 74 |
| S1 | 43 (14) | 71 (17) | 76 (162) | 78 |
| U | 44 (9) | 67 (3) | 69 (49) | 65 |
| Overall | 34.8 (66) | 59.6 (57) | 69.5 (586) | 74.4 |

[*] Comparing the overall success in 1976 of sites which were and were not occupied in 1977 (columns 1 and 3): chi$^2$ = 31.6, df 1, $P < 0.01$.
Comparing the overall success in 1977 of sites which were and were not occupied in 1976 (columns 2 and 4): chi$^2$ = 5.7, df 1, $P < 0.05$.

**Table 34**

Persistence of site occupancy between 1976 and 1977 in relation to breeding success in 1976[*]

| | 1977 | |
|---|---|---|
| Site status and year | Occupied | Not occupied |
| All sites occupied in 1976 | | |
| Successful | 407 | 23 (5.3%) |
| Unsuccessful | 202 | 43 (17.5%) |
| Sites not occupied in 1975, but occupied in 1976 | | |
| Successful | 41 | 4 (8.9%) |
| Unsuccessful | 18 | 16 (47.1%) |

[*] Testing for heterogeneity among all sites: chi$^2$ = 26.34, df 1, $P < 0.001$. Testing the frequencies observed for sites not used in 1975 against expected distribution based on sites occupied in both years: chi$^2$ = 37.35, df 3, $P < 0.001$. Testing for heterogeneity among sites occupied in both years: chi$^2$ = 11.83, df 1, $P < 0.001$.

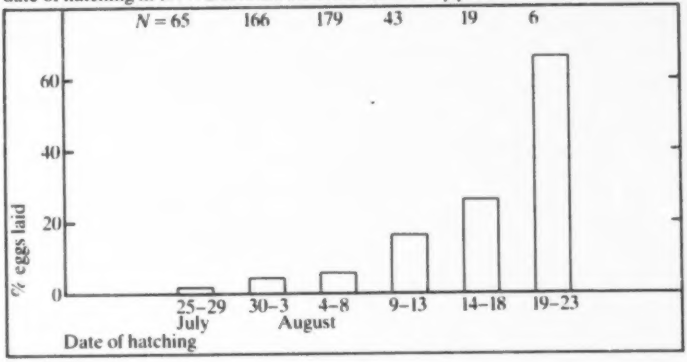
**Table 35**

Dates of hatching at plot S1 in 1977 in relation to occupancy and breeding success in 1976[*]

| | Occupied in 1976 | | |
|---|---|---|---|
| Date of hatching in 1977 | Successful | Unsuccessful | Not occupied in 1976 |
| Before 27 July | 7 | — | — |
| 27–29 July | 15 | — | — |
| 30 July – 1 August | 19 | 7 | 1 |
| 2–4 August | 27 | 6 | 3 |
| 5–7 August | 16 | 3 | 1 |
| 8–10 August | 4 | 4 | 1 |
| 11–13 August | 5 | 1 | 3 |
| 14–16 August | 4 | 1 | 2 |
| 17–19 August | — | 2 | — |
| 20–22 August | 2 | 1 | 1 |
| Totals | 99 | 25 | 12 |

[*] Comparing the dates of hatching for successful and unsuccessful sites in 1976: Mann-Whitney $U$ = 1599, $z$ = 2.25, $P$ = 0.012. Comparing occupied and unoccupied sites: Mann-Whitney $U$ = 1111.5, $z$ = 2.82, $P$ = 0.002.

**Figure 69**
Proportion of eggs which were laid on sites not occupied in 1976 in relation to the date of hatching in 1977. Dates are combined into 5-day periods



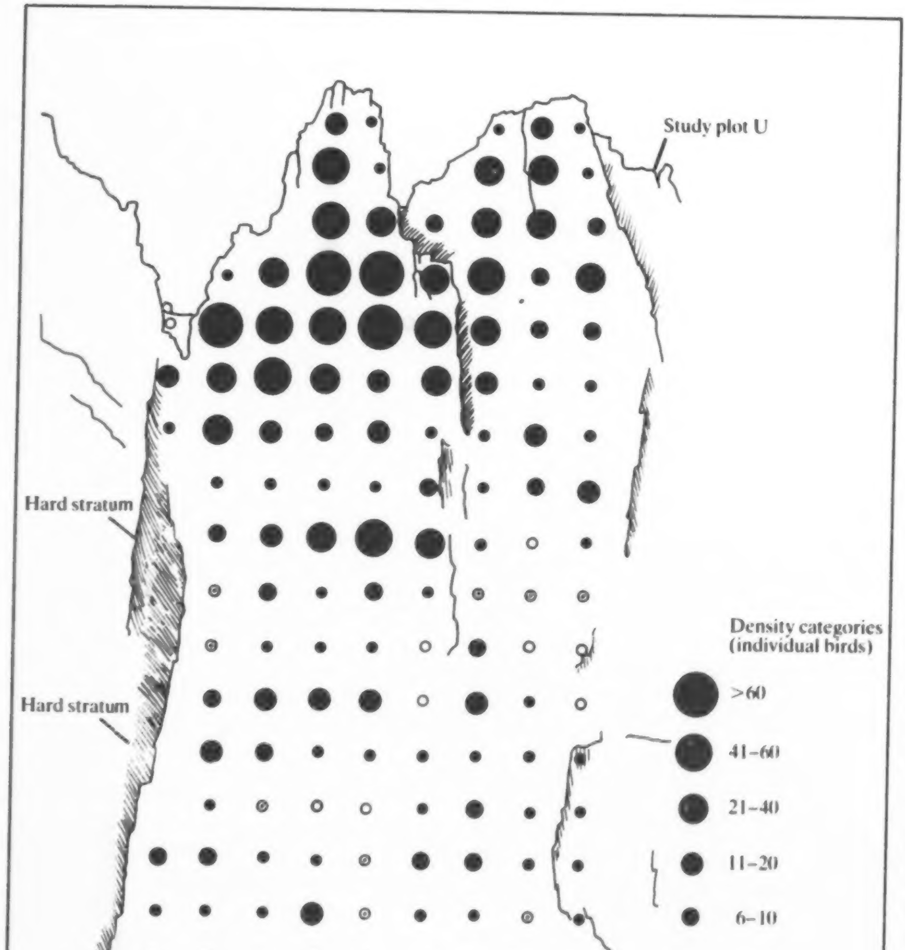
gressed (Fig. 69). Because new sites had a lower breeding success than those used the previous year, this effect could account for some of the observed seasonal decline in breeding success. The contribution was probably small, however, because based on extrapolation from hatching dates, new sites contributed only 23.5% of laying on or after 10 July, which would effect a reduction of only 3.5% in the breeding success of eggs laid during this period, compared with those laid earlier. This compares with the observed drop of about 30% (Fig. 68).

Hatchings at sites that had been unsuccessful in 1976 but that were used again in 1977, were significantly later than at sites that had been successful in 1976 (Table 35). The quality of the site, and of the birds occupying it, and the date of laying, must all be interrelated but it is not possible to distinguish the contribution of these different effects to breeding success without observations of individually recognizable birds. Because sites failing in one year tend to be unoccupied in the next, some sites occupied in consecutive years are in fact being used for the first time in the second year, having been deserted by their previous occupants and reoccupied by newcomers. If this is true, then the difference between sites occupied by the same birds in consecutive years and sites occupied for the first time must be greater than our observations imply.

### 4.2. Characteristics of the breeding site

Thick-billed Murres breeding on Prince Leopold Island occupied the entire height of the cliffs from about 6 m above sea level, but they were most dense on the East Cliff colony near the top of the cliffs and on the North Spit colony on the lower half. The height of breeding sites above the sea seems to be determined largely by the distribution of suitable ledges, with the minor indentations which scar the tops of East Cliff colony providing more sites there than on the lower areas, which are undercut in places. Hard strata, forming slight projections from the cliff face, often create local concentrations of sites, distributing the birds in horizontal bands along the cliff. The

**Figure 70**
Distribution of adult murres on a representative section of the East Cliff colony (near plot U). Actual counts are of numbers of birds present 21 July 1976 (1230 h)


Study plot U
Hard stratum
Hard stratum
Rock scree
Sea
Density categories (individual birds)
>60
41–60
21–40
11–20
6–10
1–5
no birds
? (but probably no birds)

distribution of sites on a typical section of the East Cliff colony is illustrated in Figure 70, the counts taken from census photographs.

Two principal types of ledge could be distinguished on the East Cliff colony:

(1) small, more-or-less level ledges formed by the horizontal cleavage of sedimentary rocks along their bedding planes, varying in length from a few centimetres to several metres and generally less than 15 cm wide.

(2) broader ledges, some as much as 1 m wide, sloping 30–45° towards the sea. These form from the irregular fracturing of poorly-bedded marls, which occur interbedded with the more typical calcareous siltstones, and are usually covered by a fine scree of pebbles up to about 5 cm in diameter.

An intermediate type of ledge occurred where the rock fractured into irregular blocks, forming a number of small ledges at slightly different levels. Because bands of rock with this type of fracturing ran horizontally, and because murres packed quite densely on them, they sometimes gave the appearance, at a distance, of a single ledge with several ranks of birds. Most of the sites on plot N were of this type, but in some other places they were occupied by kittiwakes.

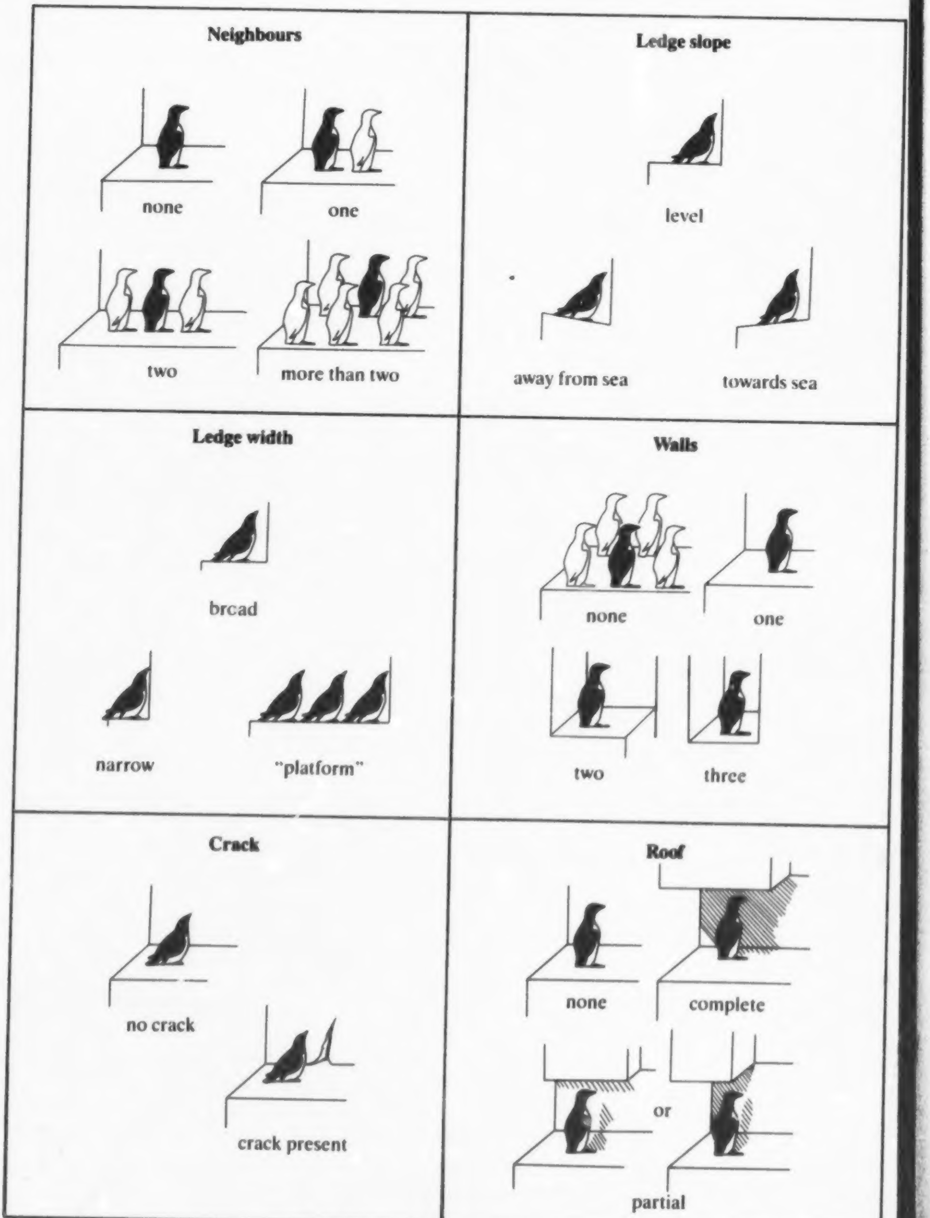
With some exceptions, ledges of the first type were occupied by murres and kittiwakes, while those of the second type were occupied by fulmars. Kittiwakes generally occupied the smallest ledges, with larger ones being taken by murres. All three species occurred more or less side by side on certain cliff faces. Interspecific competition for sites was suggested by observations of interspecific fights and the fact that some sites were used by different species in successive years.

The width of ledges occupied by Thick-billed Murres varied from a minimum of about the length of the bird's foot plus the tarsus. Many ledges were so narrow that the tail of the incubating bird hung over the edge. On the narrowest ledges, incubation changes could be made only by a lengthy manoeuvre in which the egg was transferred from the foot of one bird to the feet of the other and at one small ledge, hemmed in by walls on two sides, incubation changes were made simply by one bird deserting the egg and its partner then jumping down onto the ledge from above.

Because of the size of their egg and the position of their brood patch, Thick-billed Murres can incubate successfully only if their sternum is raised and supported during incubation. Thus the birds often breed close to a vertical cliff-face, even if the ledge is broad and flat (Williams 1974), so as to be able to press against the cliff face, resting their sternum on it and tilting their body up. Some birds will prop themselves against stones or boulders if they are available and those breeding on the seaward edge of broad ledges will use the edges of minor indentations for support. Normally, only birds without eggs will sit down flat on a ledge.

In a few places on the East Cliff colony broad, seaward-sloping ledges were occupied by murres breeding in several rows. Most of these ledges were too far from the nearest observation point for fine details of topography to be assessed, but in one case, near the top of the cliff, close examination showed that the ledge was covered in a loose scree of tabular rock fragments ranging from 2 to 10 cm thick. Breeding sites were situated along the top edges of these fragments,

**Figure 71**
Representation of breeding-site characters (1) to (6) of Thick-billed Murres, showing categories for each character


Neighbours
none
one
two
more than two
Ledge slope
level
away from sea
towards sea
Ledge width
broad
narrow
"platform"
Walls
none
one
two
three
Crack
no crack
crack present
Roof
none
complete
or
partial

which acted as small ledges tilted towards the cliff. None of the sites on the study plots was of this type.

To analyse the effect of different breeding-site characteristics on breeding success, each site on which an egg was laid in at least one season was classified by seven different characters, each character having a variable number of categories (Fig. 71):

(1) *neighbours* — the number of neighbours within half a bird's length of the sitting bird (four categories),
(2) *slope* — the angle of slope of the ledge (three categories),
(3) *width* — the width of the ledge (three categories),
(4) *walls* — the number of vertical cliff faces within one bird's length of the site (four categories),
(5) *crack* — the presence or absence of a crack or crevice in which the chick could hide when necessary (two categories),
(6) *roof* — the amount by which the ledge was immediately overhung by the cliff above, forming a roof (three categories), and
(7) *snow* — the date at which snow disappeared from the site in 1976 (seven categories).

All classifications were made by a single observer from a distance, using a telescope and usually looking obliquely downwards on the site. Because observations were made from a long range, some misclassification seems probable. A few sites had to be left unclassified.

The breeding success at all sites in all 3 years was compared separately in relation to each character. Those characters that showed significant relationships with breeding success were further compared by two-way analysis of pairs of characters to discover dependent and independent interactions. The results are given below:

(1) *Neighbours*. The number of neighbours in contact with the incubating bird might affect breeding success by reducing vulnerability to predation or by increasing accidental loss of eggs or chicks during intraspecific fights (Chapter II, section 4). Because of this we could not initially predict the effect of the number of neighbours on breeding success.

Sites with one neighbour were the most common (45.3%), those without neighbours (26.3%) or with two neighbours (25.7%) were fairly common, and those with three, rare (2.7%). Breeding success in all 3 years increased with the number of neighbours, up to two (Table 36). Birds with three neighbours had lower breeding success than those with two, probably because some of these sites were on the outer edge of groups, where the birds had no vertical wall to protect them (see below). The mean breeding success at sites without a neighbour was 7.8% less than those with one neighbour and 11.2% less than those with two neighbours. Heterogeneity between sites with nil, one, and two neighbours was significant in 1975 and 1977.

(2) *Slope*. The angle of slope of the ledge is presumably important in determining whether an egg that has been dislodged from its site remains on the ledge or falls off. We classified slope into three categories, depending on whether the ledge sloped towards the sea, away from the sea, or was more or less level and we predicted that sites sloping towards the sea would be less successful than level sites, which in turn would be less successful than those sloping away from the sea. In fact, ledges sloping away from the sea were rare (0.3% of all sites) and were therefore excluded from the analysis.

**Table 36**
Breeding success (%) of all sites in relation to the number of neighbours

| | Number of neighbours* | | | | |
|---|---|---|---|---|---|
| Year | None | One | Two | Three | *N* |
| 1975 | 70.8 (144) | 81.9 (276) | 86.3 (161) | 85.7 (14) | 595 |
| 1976 | 67.5 (157) | 69.5 (285) | 75.3 (166) | 62.5 (16) | 624 |
| 1977 | 67.3 (165) | 77.5 (284) | 77.6 (161) | 70.6 (17) | 627 |
| Mean | 68.5 | 76.3 | 79.7 | 72.9 | |

* Sample sizes are given in parentheses.
Testing for heterogeneity within years, excluding sites with three neighbours:
1975: chi$^2$ = 12.95, df 2, $P < 0.01$.
1976: chi$^2$ = 2.68, df 2, $0.3 > P > 0.2$.
1977: chi$^2$ = 6.32, df 2, $0.02 > P > 0.01$.

**Table 37**
Breeding success (%) at all sites in relation to the slope of the ledge

| | Slope of ledge* | | | |
|---|---|---|---|---|
| Year | Away from sea | Level | Towards sea | *N* |
| 1975 | 50.0 (2)† | 81.6 (309) | 81.0 (269) | 580 |
| 1976‡ | 50.0 (2) | 73.9 (333) | 63.7 (289) | 624 |
| 1977 | 100.0 (2) | 76.2 (328) | 72.9 (284) | 614 |
| Mean | — | 77.2 | 72.5 | |

* Data were excluded from the analysis (see text).
† Sample sizes are given in parentheses.
‡ Testing for heterogeneity, excluding positive slopes:
chi$^2$ = 7.74, df 1, $P < 0.01$.

**Table 38**
Breeding success (%) in relation to the width of the ledge

| | Width of ledge* | | | |
|---|---|---|---|---|
| Year | Narrow | Broad | Platform | *N* |
| 1975 | 81.1 (238) | 80.1 (226) | 80.8 (130) | 594 |
| 1976 | 68.4 (263) | 71.5 (246) | 65.9 (126) | 635 |
| 1977 | 73.3 (266) | 78.3 (226) | 71.1 (135) | 627 |
| Mean | 74.3 | 76.6 | 72.6 | |

* Sample sizes are given in parentheses. Heterogeneity within years not significant.

**Table 39**
Breeding success (%) in relation to the number of walls

| | Number of walls* | | | | |
|---|---|---|---|---|---|
| Year | None | One | Two | Three | *N* |
| 1975 | 77.1 (35) | 81.2 (373) | 80.0 (175) | 81.8 (11) | 594 |
| 1976 | 54.8 (42) | 71.5 (396) | 68.5 (181) | 60.0 (15) | 634 |
| 1977 | 60.5 (38) | 73.1 (398) | 81.6 (179) | 66.7 (12) | 627 |
| Means | 64.1 | 75.3 | 76.7 | 69.5 | |

* Sample sizes are given in parentheses.
Testing heterogeneity within years for sites with 0–2 walls:
1975: chi$^2$ = < 1, $P > 0.5$.
1976: chi$^2$ = 4.89, df 2, $0.1 > P > 0.05$.
1977: chi$^2$ = 8.31, df 2, $0.02 > P > 0.01$.

Breeding success at level sites was higher than at sites sloping towards the sea in all 3 years (Table 37), although the difference in 1975 was very small. On average, the success of sloping sites was 4.7% lower than that of level sites, the difference being significant for 1976.

(3) *Width*. The width of the ledge, like the angle of slope, affects breeding success by influencing the chance of an egg falling off once it has been dislodged from its site. The width also affects the susceptibility of the site to predation by Glaucous Gulls, although the factors involved here are probably complex (Chapter II, section 4.10). The width of the ledge also influences the number of neighbours at the site (see below). We classified site width into three categories: narrow, so that the tail of the incubating bird hung over the edge; broad, with no part of the bird hanging over; and platforms, at least two bird-lengths in width. Classification was carried out using the incubating birds as a standard measure. Narrow ledges supported the most sites (42.4%), followed by broad ledges (36.0%) and platforms (21.6%).

Little difference in breeding success was found among the three categories in 1975. In 1976 and 1977 birds on broad ledges were the most successful, followed by those on narrow ledges and then on platforms (Table 38), though heterogeneity was not significant in either year. Mean breeding success at narrow ledges was less than that at broad ledges (2.3%), as was success at platforms (4.0%).

(4) *Walls*. As well as supporting incubating birds, vertical walls adjacent to a site protect them from predation and prevent an egg that has been displaced from rolling in certain directions. A positive correlation between breeding success and the number of walls adjacent to the site was therefore expected. Relatively few sites are without a wall on at least one side (6.1%), and the majority of sites have either one (63.5%) or two (28.5%). Only 1.9% of the total sites had three walls and because those sites were often deep fissures with a complete roof they are omitted from most comparisons.

The predicted correlation between breeding success and the number of walls present was not found for any year (Table 39). Breeding success in 1975 and 1976 was highest at sites with one wall and lowest at sites without a wall in all 3 years. On average, success at sites without walls was 11.2% lower than sites with one wall and 12.6% lower than sites with two walls. Ignoring sites with three walls, heterogeneity between categories was statistically significant in 1977 and approached significance in 1976.

(5) *Cracks*. Murre chicks were seen to hide themselves in cracks and/or crevices adjacent to their site in a few instances when both parents were temporarily absent. This behaviour might enable chicks to escape from predators under certain circumstances, although chicks did not use some cracks near sites. We were unable to determine whether those cracks were unsuitable for hiding or if behaviour differed among chicks. Thus, in classifying sites on the presence or absence of a crack some misclassification seems inevitable, although cases where an obviously suitable crack was unused were rare. Only 5.8% of all sites examined were classified as having suitable cracks.

Breeding success at sites with cracks was higher than at those without cracks in all 3 years, although the differences were not statistically significant (Table 40). On average, sites without cracks were 8.0% less successful than those with cracks.

**Table 40**
Breeding success (%) in relation to the presence or absence of a crack in which the chick can hide

| Year | Cracks* |  | N |
|---|---|---|---|
|  | Present | Absent |  |
| 1975 | 85.7 (35) | 80.5 (544) | 579 |
| 1976 | 75.0 (36) | 68.1 (587) | 623 |
| 1977 | 85.7 (35) | 73.8 (568) | 603 |
| Means | 82.1 | 74.1 |  |

* Sample sizes are given in parentheses. Heterogeneity within years was not significant.

**Table 41**
Breeding success (%) in relation to the extent to which sites were roofed

| Year | Extent of roof* |  |  |  | N |
|---|---|---|---|---|---|
|  | None | Partial | Complete | Partial complete |  |
| 1975 | 80.8 (504) | 80.6 (72) | 72.2 (18) | 78.9 | 594 |
| 1976 | 68.6 (538) | 72.0 (75) | 80.0 (20) | 73.7 | 633 |
| 1977 | 75.0 (531) | 80.3 (76) | 36.8 (19) | 71.6 | 626 |
| Means | 74.8 | 77.6 | 63.0 | 74.7 |  |

* Sample sizes are given in parentheses.

**Table 42**
Breeding success (%) in all three seasons in relation to the timing of disappearance of snow from breeding sites in 1976*

| Year | Snow gone by |  |  |  |  | Present & covered, 1976 |  |
|---|---|---|---|---|---|---|---|
|  | 30 May | 5 June | 13 June | 19 June | 3 July | 3 July | 13 July |
| 1975 | 79.5<br>(117) | 82.9<br>(129) | 83.0<br>(147) | 67.3<br>(49) | 75.5<br>(53) | 82.5<br>(57) | 80.9<br>(47) |
| 1976 | 77.2<br>(127) | 67.4<br>(135) | 73.3<br>(165) | 64.4<br>(45) | 75.9<br>(54) | 71.9<br>(57) | 27.5<br>(51) |
| 1977 | 69.9<br>(123) | 75.4<br>(130) | 75.3<br>(158) | 75.6<br>(45) | 83.6<br>(55) | 75.9<br>(58) | 80.9<br>(47) |
| Means | 75.5 | 75.2 | 77.2 | 69.1 | 78.3 | 71.2 | 63.1 |
| 1976 S1 only | 84.6<br>(13) | 86.4<br>(22) | 82.6<br>(23) | 76.9<br>(13) | 76.6<br>(47) | 76.8<br>(56) | — |

* Sample sizes are given in parentheses.

(6) *Roof*. Rock falls are common on the cliffs at Prince Leopold Island once temperatures rise above freezing, and mortality of adults, chicks, and eggs from such falls was noted on a number of occasions in all years. Incubating birds reacted to the sound of rocks falling nearby by pressing themselves closely against the cliff face. Sites which were overhung by the cliff above would probably be protected from this danger. A roof might also prevent or limit the accumulation of snow and perhaps reduce the accessibility of the site to gull predators. A positive association between the presence of a roof and breeding success was therefore predicted.

In classifying sites for this character, an overhang had to be within 1 m of a site to be judged a roof. In some cases, particularly where the roof slanted, the extent of cover was difficult to determine. Of the total number of sites examined, 84.9% did not have a roof, 12.0% had a partial roof, and 3.1% were covered completely.

The predicted correlation between breeding success and the presence of a roof was found only in 1976 (Table 41). The mean success of sites with partial or complete roofs over the 3 years was almost identical to that of sites without roofs. Thus, it appears that the presence of a roof did not have any marked influence on breeding success, although sites with complete cover were too few for us to draw any firm conclusions.

(7) *Snow*. During May in all 3 years snow lay on the upper parts of the cliffs, covering most sites on plots G1, N, Q1, S1, and U. In 1976, the year when snow persisted longest, the snow melted so rapidly that 87% of all sites were clear of snow by 19 June, the day before the start of egg laying. However, on 3 July, by which time 66% of all first eggs had been laid, 9% of sites were still covered by snow.

In 1976 and 1977 a number of eggs, particularly those on plot S1, were laid on snow. Several of these slipped off the laying site and were not recovered or incubated. In other cases, the incubating bird melted a hollow in the snow, in which melt-water accumulated so that the egg was partially submerged. These eggs did not hatch.

Breeding success at sites covered in snow at the start of egg laying can therefore be expected to be lower than at other sites. Birds occupying sites covered in snow during the pre-laying period might also be at a thermal disadvantage compared to those on dry sites, especially once the temperature rises above freezing. Snow on the site may result in more energy expended on thermoregulation, which could slow down the accumulation of reserves for developing the egg. Because breeding success is related to the date of laying (this chapter, section 3.3), this may also reduce the success for birds at snow-covered sites.

There is little evidence of the predicted relationship between breeding success and the date of disappearance of snow in 1976 (Table 42). All except eight of the sites on which snow remained beyond 19 June were on plot S1, however, and figures for this plot alone for 1976 suggest sites still covered in snow on 19 June had lower breeding success than others. Many of the eggs laid on the snow at this plot were relaid and the success of these replacements was high, which suggests that sites frequently covered in snow at the time of egg laying may possess certain compensating advantages.

**Table 43**
Timing of laying of first eggs on study plot S1 in 1977 in relation to the date of disappearance of snow from the site

| Time of disappearance of snow | No. of sites | Mean laying date of first eggs (Day 1 = 1 June) |
|---|---|---|
| 30 May | 11 | 32.5 |
| 5 June | 11 | 32.5 |
| 13 June | 14 | 34.3 |
| 19 June | 7 | 33.0 |
| 3 July | 28 | 32.9 |
| 13 July | 27 | 31.7 |
| After 13 July | 6 | 39.7 |

On 13 July 1976 an unseasonal snow storm deposited snow to a depth of 50 cm on 51 sites on plot Q1. The success of these sites was only 27.5% compared with a success of 53.5% ($N = 45$) at other sites on the same plot ($\text{chi}^2 = 6.29$, df 1, $P < 0.02$). Many birds apparently deserted their eggs to avoid being buried in snow. The sites covered with snow during this storm had better breeding success in 1975 and 1977 (80.9% in both years) than other sites (76.6 and 67.4%, respectively). This again suggests that sites prone to the accumulation of snow may have other advantages.

A comparison of the mean dates of laying of first eggs on plot S1 in relation to the disappearance of snow is given in Table 43. Only at sites where snow was still present on 13 July is there any indication that snow may have delayed egg laying and no overall trend is apparent. Thus, if snow does exert an effect in delaying the onset of egg laying, it must be masked by other factors.

### 4.3. Combined effects of breeding-site characters

Of the seven breeding-site characters examined, crack, roof, and snow will not be considered further because of their apparently insignificant effect on breeding success. We examined the effect of each of the other four on breeding success when other characters were held constant, taking the characters two at a time. We prepared separate matrices for each season and calculated from these the mean success of each cell. To reduce the size of matrices, sites with two and three neighbours were combined and those sloping away from the sea and those with three walls omitted, so that all matrices were either three by three or two by three cells.

In the presentation of the matrices the direction of inequalities is indicated (Tables 44–46). Where these directions are the same as those predicted by the previous one-way analyses, the effects of the two characters can be assumed to operate independently. The distribution of sample sizes in each cell can also be compared with the marginal totals to determine whether the two characters occur independently. Where they do not, the apparent differences in breeding success between categories revealed in the one-way analyses may be partly determined by inter-correlation with the other character.

Comparisons of breeding success for sites with different numbers of neighbours, controlling for walls, width, and slope separately, are given in Table 44. Since breeding success in both rows and columns increases in the predicted directions, the effects of neighbours and

**Table 44**
Breeding success in relation to the number of neighbours, controlling for walls, width, and slope. Figures in each cell are the mean success over three seasons

| | No. of neighbours* | | | | |
|---|---|---|---|---|---|
| Item | None | | One | | Two & three |
| Number of walls | | | | | |
| None | 62.7(12) | < | 64.9(13) | ≃ | 64.8(13) |
| | ∧ | | ∧ | | ∧ |
| One | 63.0(75) | < | 76.1(187) | < | 80.1(136) |
| | ∧ | | ∧ | | ∧ |
| Two | 72.7(66) | < | 78.3(75) | < | 81.0(27) |
| Width of ledge | | | | | |
| Broad | 70.0(54) | < | 77.8(95) | < | 79.8(77) |
| | ∨ | | ∨ | | ∨ |
| Narrow | 66.8(92) | < | 76.8(120) | < | 79.5(54) |
| | ∨ | | ∨ | | ∨ |
| Platform | 60.5(19) | < | 74.1(69) | < | 76.5(47) |
| Slope of ledge | | | | | |
| Towards the sea | 69.3(77) | < | 70.8(123) | < | 78.1(84) |
| | ∨ | | ∧ | | ∧ |
| Level | 65.8(84) | < | 80.4(159) | > | 80.0(85) |

* Sample sizes are given in parentheses.
Testing for independence between site characters:
Neighbour vs. walls, $chi^2 = 35.3$, df 4, $P < 0.001$.
Neighbour vs. width, $chi^2 = 29.0$, df 4, $P < 0.001$.
Neighbour vs. slope, $chi^2 = 1.9$, df 2, $P > 0.1$.

**Table 45**
Breeding success in relation to the number of walls, controlling for width and slope. Figures in each cell are the mean success over three seasons. Sites with three walls are omitted

| | No. of walls* | | | | |
|---|---|---|---|---|---|
| Item | None | | One | | Two |
| Width of ledge | | | | | |
| Broad | 61.7 (10) | < | 76.5 (139) | < | 79.1 (77) |
| | ∨ | | ∨ | | ∨ |
| Narrow | 58.6 (10) | < | 74.8 (168) | = | 74.8 (88) |
| | ∧ | | ∨ | | ∨ |
| Platform | 66.7 (18) | < | 74.2 (91) | > | 70.8 (26) |
| Slope of ledge | | | | | |
| Towards the sea | 63.7 (23) | < | 72.7 (184) | < | 75.4 (77) |
| Level | 70.5 (13) | < | 77.3 (204) | > | 76.9 (111) |

* Sample sizes are given in parentheses.
Testing for independence between site characters:
Walls vs. width, $chi^2 = 23.1$, df 4, $P < 0.001$.
Walls vs. slope, $chi^2 = 6.3$, df 2, $0.05 > P > 0.02$.

**Table 46**
Breeding success in relation to width, controlling for slope. Figures in each cell are the mean success over three seasons

| | Width of ledge* | | | | |
|---|---|---|---|---|---|
| Slope of ledge | Broad | | Narrow | | Platform |
| Level | 81.1 (127) | > | 74.8 (163) | < | 77.4 (38) |
| | ∨ | | ∨ | | ∨ |
| Towards the sea | 72.0 (92) | < | 73.2 (99) | > | 72.6 (93) |

* Sample sizes are given in parentheses.
Testing for independence between site characters:
Width vs. slope, $chi^2 = 41.0$, df 2, $P < 0.001$.

walls appear to operate independently, although the effect of neighbours at sites without walls appears negligible. The occurrence of the two characters is related, however, since sites with one wall have no neighbours less frequently and two or three neighbours more frequently than would be expected if they occurred independently. This association has the effect of increasing the apparent success of sites with one wall relative to those with two walls in Table 39 because of the over-representation of sites with two or three neighbours.

The direction of inequalities is also constant when neighbour categories are compared with width held constant (Table 44), but again the occurrence of the two characters is related, so that narrow ledges have a higher proportion and platforms a lower proportion of sites without neighbours than would be expected. This biases the apparent success on narrow ledges downwards and that on platforms upwards (Table 38). For sites with one or more neighbours, the success of those on narrow ledges is very similar to that of those on broad ledges.

The comparison of breeding success between neighbour categories, controlling for slope, gives a less consistent picture, since pairs at sites without neighbours were more successful where the site sloped towards the sea than where it was level, the reverse of the trend suggested by the one-way analysis of slope (Table 37). The effect of slope demonstrated in Table 37 apparently applies mainly to sites with one neighbour, which constitute 45% of the total.

The effect of walls on breeding success was consistent for both broad and narrow ledges, but not for platforms, although this difference was not statistically significant (Table 45). The two characters were not independent in their occurrence because sites without walls were more frequent on platforms and sites with two walls more frequent on broad ledges than would be expected if they occurred independently. This must exaggerate the apparent difference between platforms and other ledges in Table 38.

The relationship between walls and breeding success with slope constant was as expected, except that at level sites the success of those with two walls was lower than those with one wall. Although the two characters were not distributed independently, the level of significance ($0.02 > P > 0.05$) suggests that the association is relatively slight.

Breeding success in relation to width, with slope held constant, showed a different pattern of inequalities from that predicted by Tables 37 and 38. For sites sloping towards the sea, narrow ledges were the most successful, but differences were small and not statistically significant (Table 46). For level sites, narrow ledges were least successful and broad ledges most successful.

Slope and width were strongly interdependent with a much higher proportion of platforms sloping towards the sea (71%) than other widths (40%). This would tend to bias the success of platform sites downwards in Table 38 and accounts for the apparently poorer success of platforms compared with narrow ledges. Thus, most of the effect of ledge width, as defined here, is due to its relationship with slope and this partly explains why the positive correlation predicted initially between the width of the ledge and breeding success was not apparent in Table 38.

Apart from snow, which apparently affected only plots Q1 and S1, most of the variation in breeding success attributable to breeding-site characters is due to three characters: neighbours, walls, and slope. In the case of neighbours and walls the greatest difference was between sites with none and those with one, the difference between sites with one and two being smaller. Thus, the most successful type of site is one on a level ledge, protected by one or more vertical faces, and contiguous with at least one other site.

The proportions of sites for each plot falling into each category for neighbour, walls, and slope (App. 21) were used to prepare an index predicting the relative breeding success of the seven study plots. The index chosen was the product of the proportion of sites without neighbours, without walls, and with negative slope (Table 47). A significant correlation was found between this index and the mean ranking of sites by breeding success over the 3 years ($r_s = 0.875$, $N = 7$, $P < 0.05$). For 1977 the correlation was better ($r_s = 0.937$, $P < 0.01$) and a major portion of the difference in mean ranking was contributed by plot Q1, the success of which was drastically affected by snow in 1976. Although there is an element of circularity in this comparison, it does emphasize the point made earlier, that differences between plots are probably best explained in terms of the characteristics of their constituent sites.

Allowing for the fact that probably not all the characters affecting breeding success were taken into consideration and assuming that a significant proportion of sites were misclassified due to difficulties with the technique and constraints imposed by working at long range, most of the observed difference in breeding success between plots probably can be explained by differences in the proportion of different types of site.

Because sites vary significantly in quality, we should expect competition to be highest for those sites conferring the greatest advantage; specifically, those sites situated adjacent to one or two walls, with neighbours, and on level ledges. This competition might result in differences in the quality of birds occupying different sites and we might predict that good quality sites would be occupied by good quality birds. This would tend to accentuate the effects of site quality on breeding success, since the quality of site and bird would tend to be additive. An alternative hypothesis is that competitive ability for obtaining breeding sites is independent of the ability to reproduce successfully (e.g., the ability to obtain a good site might depend on

**Table 47**
Index of predicted breeding success for seven study plots compared with observed breeding success. The index is calculated as the product of the proportion of sites on each plot having no walls, no neighbours, and sloping toward the sea*

| | Study plot | | | | | | |
|---|---|---|---|---|---|---|---|
| Item | G1 | G4 | N | Q1 | Q4 | S1 | U |
| Index | 0 | 0.035 | 0.003 | 0.007 | 0.003 | 0.005 | 0.015 |
| Ranks | 1 | 7 | 2.5 | 5 | 2.5 | 4 | 6 |
| Mean rank in breeding success | 1 | 6.5 | 2 | 6.5 | 4 | 3 | 5 |

* Spearman rank correlation coefficient ($r_s$) = 0.875, $N = 7$, $P < 0.05$.

the strength of the male, whereas the ability to lay early might be related to the size of the female), in which case the reproductive quality of birds would be distributed randomly in relation to breeding-site characters.

To examine these two conflicting hypotheses, we used the date of hatching as a measure of the laying date and, hence, of the quality of the female, assuming that good quality females are capable of laying earlier than poor quality females. We preferred the date of hatching to the date of laying because of the larger sample size available. Mean dates of hatching for each plot, broken down into categories by neighbours, walls, and slope are given in Table 48.

There is some indication that birds with two neighbours lay earlier than those with no neighbours or one neighbour. Although this holds for all plots when one and two neighbours are compared, there are two plots (Q1, S1) where sites without neighbours laid earlier than those with two. The relationship between slope and hatching date is more consistent; sites on the level hatch earlier than those on a slope at all plots except Q1, where the difference was insignificant ($P = 0.65$).

Differences in mean hatching date in relation to the number of walls are quite different from those predicted by breeding success on the first hypothesis, i.e., early laying birds will occupy the best sites. Eggs at sites without walls or only one wall hatched earlier on all plots than those with two walls except on plot Q1. On three plots, birds at sites without a wall laid earlier than those with one wall. This anomaly can be explained by the hypothesis that sites with two walls tend to receive less direct sunlight than those with one or none and that this puts females occupying these sites at a thermal disadvantage during the period when they are developing the egg. By the same token, birds which have one or two neighbours may gain some thermal advantage from their proximity. Differences in microclimate between sites could also influence the length of the incubation period and, hence, the date of hatching. In any case, the figures suggest that reproductive quality, as measured by hatching date, is not independent of breeding-site characteristics.

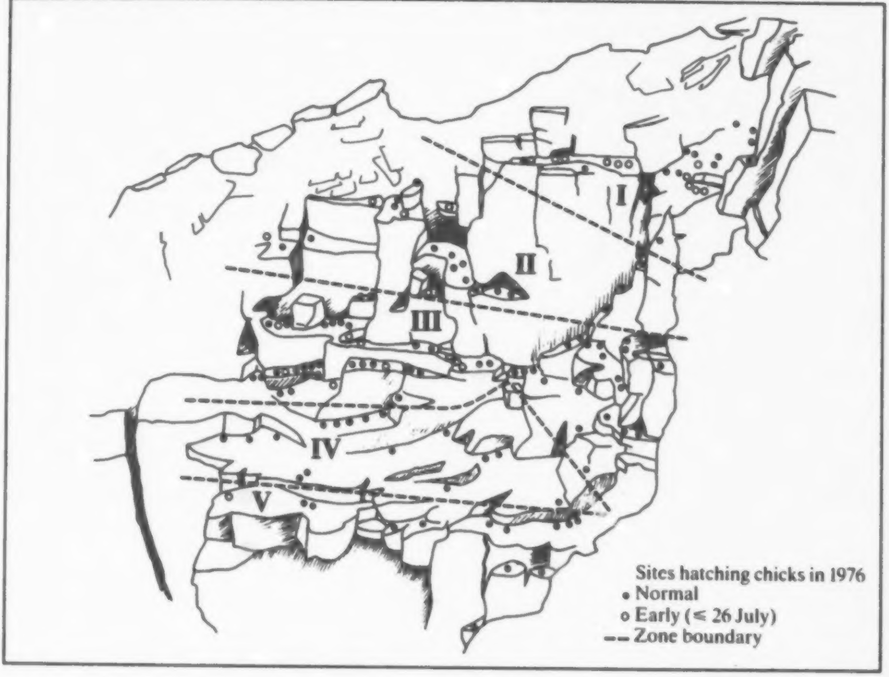
We examined the relationship between date of hatching and the nature of the site from another perspective by analysing the distribution of early-hatching chicks on plot S1 ("early" defined in this chapter, section 2.2). Superficial inspection suggests that chicks were

**Table 48**
Mean dates of hatching in 1977, broken down by neighbour, wall, and slope categories (day 1 = 1 June)*

| Study plot | No. of neighbours | | | | No. of walls | | | | Slope of ledge | |
|---|---|---|---|---|---|---|---|---|---|---|
| | None | One | Two | Three | None | One | Two | Three | Towards the sea | Level |
| G1 | 66.6(11) | > 63.4(17) | > 62.0(1) | 67.0(1) | | 63.0(26) | < 65.2(17) | | 64.6(19) | > 63.3(24) |
| G4 | 63.4(13) | = 63.4(22) | > 63.3(6) | | 63.0(6) | > 62.2(20) | < 65.3(13) | 64.0(2) | 63.8(28) | > 62.5(13) |
| N | 65.0(20) | < 65.7(32) | > 62.5(17) | | 68.5(2) | > 62.9(47) | < 69.1(18) | 64.0(2) | 67.0(22) | > 63.6(47) |
| Q1 | 64.8(23) | < 66.6(34) | > 66.5(17) | | 69.3(3) | > 65.9(44) | = 65.9(27) | | 66.5(24) | > 65.9(50) |
| Q4 | 64.6(11) | > 63.9(28) | > 62.0(26) | 70.0(2) | 61.0(2) | < 63.3(46) | < 64.1(18) | 68.0(1) | 62.9(47) | < 64.8(20) |
| S1 | 64.4(29) | < 65.4(65) | > 65.2(40) | 65.3(6) | 61.8(5) | < 65.1(91) | < 65.9(40) | 62.2(4) | 66.4(55) | > 64.4(74) |
| U | 66.4(8) | > 65.7(19) | > 62.8(6) | 67.2(4) | 62.4(5) | < 65.0(22) | < 68.2(10) | | 66.0(12) | > 65.3(25) |
| Means | 65.0 | 64.9 | 63.5 | | 64.3 | 63.9 | 66.2 | | 65.3 | 64.3 |

* Sample sizes are given in parentheses.

**Figure 72**
Sketch showing the distribution of early-hatched chicks on plot S1 in 1976



more likely to hatch early on certain parts of the plot, particularly the narrow ledges at the top (zones I and II in Fig. 72) and the broad system of ledges running across the centre of the plot (zone III). In contrast, chicks on the sloping platform area (zone IV) rarely hatched early. The difference between zones was similar in all 3 years (Table 49), but heterogeneity was significant only in 1976. The results from different years are not independent, however; the relatively high proportion of early-hatching chicks in zone I was determined in all 3 years by a small group of consistently early sites on narrow, level ledges (group "X" shown in Fig. 73). Other factors, in addition to those measured, probably contribute significantly to the observed variation in laying dates.

### 4.4. Discussion of breeding success

Compared with other studies of breeding success in arctic murres (Uspenski 1956, Tuck 1961, Belopol'skii 1957, Swartz 1966, Johnson and West 1975), the success of reproduction estimated for the Prince Leopold Island colony in all 3 years was high. The difference probably relates to the differences in methods already mentioned. Birkhead (1976*a*) recorded a similar level of success for the Common Murre, as did Lloyd (1976) working on Razorbills; both used the same technique as ours.

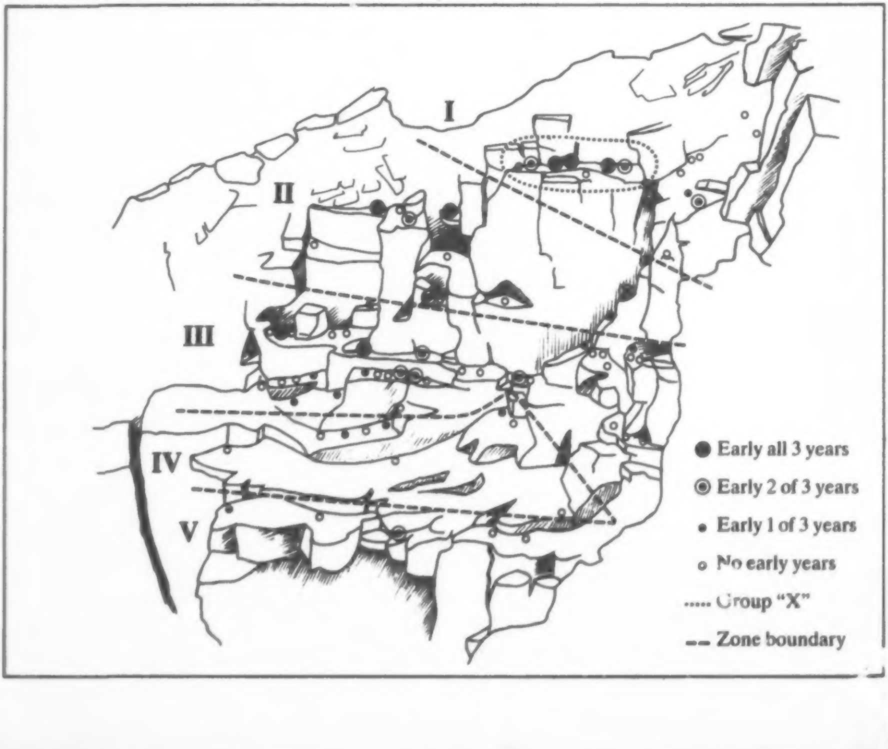
A comparison of breeding success with the timing of laying shows that birds which lay at the end of the laying period reduce their chances of fledging a chick successfully by about 50%, compared with birds laying at the peak. Presumably once their chances fall below this level they do not attempt to lay, suggesting that at this point the possible gain to the residual reproductive value of the bird through rearing a chick is counterbalanced by a possible reduction in the parent's life expectancy due to lowered survival during the following winter. Using demographic parameters already defined, we can esti-

**Table 49**
Proportions of chicks hatching early in five zones on plot S1 (see Fig. 72). Early chicks are defined as those hatching in the first 4 days in 1975 and 1976 and the first 6 days in 1977

| | Proportion of early-hatching chicks, % * | | |
|---|---|---|---|
| Zone | 1975 | 1976 | 1977 |
| I | 35 (17) | 46 (24) | 24 (21) |
| II | 35 (90) | 27 (22) | 32 (19) |
| III | 23 (57) | 11 (61) | 14 (59) |
| IV | 13 (23) | 0 (16) | 9 (22) |
| V | 18 (17) | 8 (13) | 14 (14) |
| Heterogeneity chi$^2$ † | 4.45 | 16.81 | 4.51 |
| *P* | N.S. | <0.001 | N.S. |

* Values in parentheses are sample sizes.
† Lumping zones I and II, and zones IV and V.

**Figure 73**
Sketch showing the distribution of early-hatched chicks (≤ 26 July) on plot S1 in 1975, 1976, and 1977, and all sites where the date of hatching was recorded in all 3 years



mate this potential decrease in survival as about 5% of the normal annual survival rate for adults (Table 50). This figure is likely to be a maximum estimate, however, because a chick reared at the end of the season probably has less likelihood of surviving subsequently than one reared earlier and, hence, its value to the parent is correspondingly lower.

The tendency for particular sites to have similar success from year to year may be compounded by a number of factors. Because of the high degree of site-tenacity, part of the effect must be due to the particular quality of the birds occupying the site, and part to the quality of the site itself. As already noted, these two qualities are likely to be correlated. Because there is a tendency to desert an unsuccessful site, we can assume that some of these sites will be occupied the next year by pairs breeding for the first time; and, since these young birds are likely to be unsuccessful, the tendency for successive failures at the same site will intensify.

Success in relation to characteristics of the breeding site has been discussed in detail for Common Murres by Birkhead (1977*a*), who found that density, dependent partly on the size of the ledge, was an important determinant. Kaftanovskii (1938) also found murres breeding in dense aggregations to have a higher breeding success than birds which were more spaced out, due to the differential effects of gull predation. Johnson (1941) found the position of laying sites in relation to the centre of a particular subcolony was related to the date of laying. Variation in density among Common Murres, however, is much greater than among Thick-billed Murres, since they frequently occupy ledges in several ranks and have evolved posture displays enabling birds with sites in the inner ranks to pass the outer ranks without aggression (Tschanz 1959, Birkhead 1978*a*). This situation is unusual among Thick-billed Murres, which usually form a single line on their breeding ledge, and the neighbour effect is correspondingly less important, although still present.

**Table 50**
Estimation of the potential reduction in adult survival during the subsequent year caused by late breeding

Assumption
For the latest laid eggs, the average increase in reproductive output (chicks fledged per egg) is equal to the loss of future output due to a reduction in the average rate of survival during the subsequent year.

Parameters

| | |
|---|---|
| Normal annual adult survival ($s$) | 0.91 (Birkhead and Hudson 1977) |
| Normal breeding success ($r$) | 0.73 chicks/year |
| Minimum acceptable breeding success ($r'$) | 0.40 chicks/year |
| Future life expectancy ($L$) | 7.36 years ($s^L = 0.5$) |

Let $s'$ be the mean adult survival when laying is attempted at the point of minimum acceptable breeding success

Then $s's^x = 0.5$
Where $x = L - 1 - (r'/r)$
Hence $s' = \dfrac{0.5}{0.91^{(7.36-1-0.4/0.73)}}$
$= 0.865$
Hence, expressing $s'$ as a percentage of $s$ = 95%

Much of the observed variation in breeding success can be related to physical characteristics of the sites. Some of these, such as angle of slope and the number of protective walls, can be monitored immediately by the birds, whereas others, such as the susceptibility of the site to the accumulation of snow or to gull predation, may be more difficult to assess. The tendency to desert a site that is unsuccessful, however, ensures that areas only marginally suitable for breeding and where drawbacks are not immediately apparent, do not become permanently colonized. The difference between sites occupied in successive years and those not occupied in the previous year may relate to the age of the birds, because new sites are more likely to be occupied by young birds breeding for the first time and these birds probably lay later and are less successful than older birds (Krasovski 1937, Ashcroft 1976, Lloyd and Perrins 1977, Brooke 1978). The high rate of change for sites occupied for the first time indicates that young birds are probably more prone to shift after a failure than older birds. Birds probably change their site if they fail in their first year of breeding and they may continue to do so until they succeed, so that the period of site selection is probably lengthy and includes a process of trial and error.

Exposure to potential rock falls must be an important factor in the selection of a breeding site; and, although it could not be measured, the qualitative observation that birds were absent from the lower parts of gullies on the east cliffs, which tended to channel rock falls, supports this view. Rock falls regularly cause adult mortality and in a potentially long-lived species such as the Thick-billed Murre [minimum annual adult survival 91% (Birkhead and Hudson 1977)], even a small risk would outweigh a considerable advantage in breeding success. Rock falls may be largely responsible for the concentration of the population on the east cliffs in the uppermost 100 m, despite the presumed thermal disadvantage compared to areas lower down.

A comparison of breeding success over the 3 years of the study shows considerable uniformity, if we except localized disasters such as that which occurred on plot Q1 in 1976. We saw no chicks die of starvation in any year, but patterns of chick-growth are extremely flexible (Chapter IV) and clearly adjust to widely varying food supplies. Fledging in the semi-precocial murres cannot be taken as equivalent to fledging in nidicolous species, since they leave the cliffs at only 20–25% of adult weight (Johnson and West 1975). Tuck (1961) mentions heavy mortality of chicks immediately after fledging during storms at Akpatok Island and Digges Sound, with hundreds of corpses washed ashore. This type of mortality is probably less consistent from year to year than egg and chick mortality on the breeding site; therefore, despite the observed similarity in breeding success from year to year, recruitment into the adult population may vary considerably, reflecting post-fledging mortality. This in turn may be related to the weight of the chicks at fledging and hence to nutrition during chick rearing.

Some estimate of the mortality that occurs between fledging and reaching the wintering grounds of the population can be obtained from band recoveries for murres banded as chicks. In 1955 L.M. Tuck banded 2000 adults and 8000 chicks at the Thick-billed Murre colonies in Digges Sound. No recoveries of birds banded as chicks were reported from the vicinity of the colony in that year, presumably because mortality took place along the virtually uninhabited coasts of Hudson Strait and Labrador. An estimate of the "missing mortality" occurring between the colony and the wintering grounds off Newfoundland can be obtained indirectly (Table 51), however, and suggests that only 40% of chicks completed the journey and joined the "recoverable" population off Newfoundland. A similar calculation, based on 2500 birds banded at Cape Hay in 1957, yields a figure of 39% for the proportion of chicks surviving. If the bulk of the mortality involved occurred before the chicks had reached adult size, the reproductive success of the population in terms of fully grown young is only about one-third of the apparent success calculated in terms of young fledging from the colony and probably represents only about 0.25 young per pair annually.

**Table 51**
Estimate of post-fledging mortality occurring between fledging (August) and arrival on the wintering grounds off Newfoundland (November), based on data derived from L.M. Tuck's banding of Thick-billed Murres at Digges Sound in 1955

| | |
|---|---|
| Assumptions | |
| Annual survival of adults banded as breeders (Birkhead and Hudson 1977) | 91% ($s$) |
| Survival up to 5 years (calculated from CWS banding data from Digges Sound using the method described by Lack 1961) | 15% ($s'$) |
| Age of first breeding (Birkhead and Hudson 1977) | 5 years |
| Data from the Digges Sound banding program | |
| Total adults banded | 2000 ($A$) |
| Total chicks banded | 8000 ($N$) |
| Total adults recovered from 1960 onwards | 21 ($a$) |
| Total chicks recovered from 1960 onwards | 8 ($n$) |
| 1. Estimate of number of chicks surviving in 1960 based on the subsequent proportions of adults to chicks among all recoveries. This assumes that after the initiation of breeding the behaviour of birds banded as chicks was identical to that of birds banded as adults. | |
| Number of adults surviving in 1960 = $A.s^5$ = | 1248 |
| Hence estimated number of chicks surviving = $A.s^5.\frac{n}{a}$ = | 475 ($X$) |
| 2. Estimate of number of chicks surviving in 1960 based on survival rates derived from recovery data. | |
| Estimated number of chicks surviving = $N.s'$ = | 1200 ($X'$) |
| 3. Estimated survival between fledging and joining the recoverable population | |
| $= \frac{X}{X'} =$ | 40% |

## 5. Summary

(1) Breeding success was monitored by observing selected study plots from a distance and determining dates of laying, hatching, and fledging by noting the presence or absence of eggs and chicks. The method was more accurate for determining hatching and fledging dates than for laying and tended to underestimate the number of breeding pairs and overestimate breeding success. The error involved was probably small and dependent on the duration of observation. Results for 1977, when sample sizes were smaller and more observers were available, were probably more accurate than those for other years.

(2) First eggs were seen in all 3 years on 20 or 21 June. Median laying dates fell between 28 June and 3 July, 1975 being the earliest and 1977 the latest year.

(3) Incubation lasted 31–34 days and the chicks fledged at 15–30 days old, most between 18 and 23 days old.

(4) Eggs lost or predated took 11 to 17 days to replace and the proportion replaced fell during the season from more than 80% of those lost in June to only 30% by mid July. None were relaid after 22 July.

(5) The age of chicks at fledging declined as the season progressed, but there was considerable variation owing to adverse weather conditions, which delayed some cohorts.

(6) Evidence from the skewed distribution of laying dates and other observations suggests that in some years part of the population does not lay immediately it becomes capable of doing so, timing apparently being determined by other factors. This leads to greater synchrony of laying within the population, which confers advantages in avoiding predation.

(7) The hatching success of first eggs varied between 76 and 84% over the 3 years and 87–94% of chicks that hatched survived a minimum of 14 days, after which age they were considered to have fledged. Overall breeding success, including relays, ranged from 68 (1976) to 79% (1975), but mortality immediately after fledging is probably heavy.

(8) Both hatching and fledging success declined with date of laying, the earliest eggs being generally the most successful. The decline was not uniform but affected particularly the latest 20% of the eggs to be laid.

(9) Comparisons of breeding success among study plots showed that success tended to be similar from year to year and the same applied to individual sites.

(10) Sites that were occupied in all 3 years were generally more successful than others. Sites unsuccessful in one year were less likely to be occupied the following year than were successful sites.

(11) Breeding success was influenced by characteristics of the laying sites, including the slope and width of the ledge, the number of adjacent walls, and the number of close neighbours. Site characteristics were also interrelated, and much of the observed variation in breeding success could be attributed to their combined effects.

# Chapter IV Development of young

# 1. Introduction

Because of their potential value as indicators of the availability of food at different stages of the breeding cycle, we measured the size of eggs and the rate of growth and fledging weight of chicks at Prince Leopold Island in all 3 years of the study. The rate at which chicks increase their weight is a useful measure of the provisioning ability of their parents, which in turn is dependent on the availability of suitable food and feeding conditions. The size of the egg is determined by a number of factors, including the nutritional state of the female immediately prior to laying, and hence it affords some measure of the availability of food during the pre-laying period (Bryant 1978*a*). Chick growth is also related to egg weight, because chicks from large eggs can develop faster than those from small eggs (Schifferli 1973, Lloyd 1976, Bryant 1978*b*, O'Connor 1978). Differences in growth rates will probably affect the age and/or condition of the chick at fledging and this is an important determinant of post-fledging survival in a number of species of seabirds (Perrins *et al*. 1973, Jarvis 1974).

If the principal factor limiting the rate of growth of the chicks is the ability of parents to supply them with food, then observations of feeding rates should provide a convenient measure of the nutritional state of the chicks. The effect of rates of feeding on chick growth is mediated by the size of the meals supplied, however, as a bird that spends a long time foraging for food can compensate for its slow rate of delivery by bringing back larger meals. In many situations, nevertheless, information on feeding rates is much easier to collect than data on growth rates. Therefore, we measured the rate at which chicks were provisioned throughout the chick-rearing period in all three seasons and analysed the relationship between feeding rate and the age of the chicks, the date, and the prevailing weather conditions.

The colour and markings of Thick-billed Murre's eggs are highly variable, as are those of the Common Murre (Drane 1898, Tschanz 1959). Among Common Murres, eggs laid on the same site tend to be the same colour and pattern from year to year (Seebohm 1882, Aspden 1928, Southern 1951), which indicates that they were probably laid by the same female. Marsault (1975) found that eggs laid by captive females exhibited the same ground colour and T.R. Birkhead (pers. commun.) also found that markings were consistent. Lloyd (1976) made similar observations on the Razorbill and found that egg colour and markings were constant even after a female had changed mates. If differences in ground colour and markings are genetically determined, as seems likely (Romanoff and Romanoff 1949), then these characters may be linked to other genetic traits, including those affecting breeding success. We tried to investigate this for the Prince Leopold Island population.

## 2. The egg

### 2.1. Methods

Eggs and chicks were measured in all years at three plots (SA, SB, SC) situated at the top of the cliff, about 20 m from plot S1. Eggs were also measured in 1975 on an area adjacent to plot U. In 1977 eggs and chicks were measured at a fourth plot close to S1 (SD) and at three plots close together on cliff E (EA, EB, EC); eggs were measured at one plot close to the base of the cliffs below A.

In 1975 plots used for growth studies were checked at 2–4 day intervals throughout egg laying, so that newly laid eggs could be weighed. The length and maximum breadth of the eggs were also measured to the nearest 0.1 mm. Because the visits during egg laying caused heavy losses, plots were visited only just before hatching in 1976, when the eggs were measured but not weighed. In 1977 plots were visited twice during the incubation period: 10 days after the start of laying and again prior to the start of hatching. Eggs were weighed and measured at the first visit and weighed again on the second visit to determine the rate of weight loss during incubation. A small sample of sites that could be checked without much disturbance was visited regularly and the eggs weighed, within 4 days of laying.

The ground colour of eggs of the Thick-billed Murre varies from almost white to dark green, the majority being bluish-green. No attempt was made to classify colour as such, but the degree of saturation of colour was classified on an arbitrary scale of five intervals: class 1, very pale green; class 2, pale green; class 3, green; class 4, bluish-green; and class 5, dark green (see Plate 14). Initially a "type collection" was carried in the field for comparison, but later the comparison was made from memory. All classifications were made by the same person (AJG) and eggs classified more than once were usually assigned to the same category each time (90% correct), so the classification was relatively consistent. Markings on eggs were classified into four categories according to shape and size: speckles (< 2 mm), spots (2–4 mm), blotches (> 4 mm), and scribbles (elongated streaks of any dimension) and into three categories of colour: pale brown, brown, and black (see Plate 15).

### 2.2. Egg weight and volume

The mean weight of eggs weighed within 4 days of laying at S and U was 98.5 g (SD = 8.08, range: 85–114, $N = 54$) in 1975 and 94.6 g (SD = 9.41, range: 63–106, $N = 19$) in 1977. The difference between the 2 years was significant ($P < 0.01$, $t = 2.68$). The rate of weight loss of 44 eggs weighed twice in 1977 at intervals between 15 and 21 days averaged 0.56 g per day, exactly the same rate found by Uspenski (1956) for Thick-billed Murres in Novaya Zemlya and very close to the rate recorded for mixed Common and Thick-billed murre eggs in Alaska by Johnson and West (1975). In both these studies, however, the eggs were heavier than Prince Leopold Island eggs, with a mean weight of 104.7 g at Novaya Zemlya and a pipping weight of 105.6 g (equivalent to 123 g fresh weight) at Cape Thomson, Alaska. Eggs laid by Thick-billed Murres on Prince Leopold Island are therefore small compared with those laid by other populations, although this may be related to the size of the adult birds.

To compare the size of eggs not weighed within 4 days of laying, an index of volume calculated as the product of the length and the square of the maximum diameter was used. This index has a linear relationship to volume and hence to initial weight (Parsons 1970). The index was significantly smaller for eggs laid in 1977 than for those laid in the other two seasons (Table 52). Volume also differed between eggs measured at S and those measured at E. The difference was not statistically significant, but all plots at U and S had a larger mean volume index than those at A and E. This appeared unrelated to the exposure and orientation of the plots, because both areas included north- and south-facing plots.

### 2.3. Egg colour

The distribution of different types of markings in relation to the ground colour of the eggs was significantly non-random (Table 53). In general, eggs with a dark ground colour had larger markings than those with a light ground colour. This also applied to the colour of the

**Table 52**
Volume indices for eggs (index = length × maximum breadth$^2$)*

| Year | Study plot | Mean | SD | *N* |
|---|---|---|---|---|
| 1975 | U(UA, UB, UC) | 188.3 | 15.1 | 39 |
| | S(SA, SB, SC) | 192.3 | 13.9 | 43 |
| 1976 | S(SA, SB, SC) | 193.9 | 16.3 | 29 |
| 1977 | U(UA, UB, UC) | 181.7 | 17.6 | 13 |
| | S(SA, SB, SC) | 181.5 | 16.0 | 77 |
| | E(EA, EB, EC) | 178.8 | 15.6 | 111 |
| | A | 178.7 | 15.9 | 22 |
| | SA | 180.7 | 11.6 | 34 |
| | SB | 185.4 | 18.0 | 13 |
| | SC | 180.6 | 19.3 | 30 |
| | SD | 184.3 | 11.6 | 37 |
| | EA | 177.9 | 21.8 | 16 |
| | EB | 179.7 | 14.8 | 82 |
| | EC | 174.0 | 14.1 | 13 |

* Comparing plots (SA, SB, and SC combined) between years: 1975 vs. 1976: $t = 0.44$, $0.9 > P > 0.5$; 1975 vs. 1977: $t = 3.89$, $P < 0.001$; 1976 vs. 1977: $t = 3.52$, $P < 0.001$.
Comparing plots within 1977: SA, SB, SC, SD vs. EA, EB, EC: $t = 1.64$, $P \simeq 0.1$.

**Table 53**
Egg markings in relation to ground colour (colour class: 1, very pale green; 2, pale green; 3, green; 4, bluish-green; 5, dark green)

| Largest markings† | Ground colour of egg* | | | | Totals |
|---|---|---|---|---|---|
| | 1 and 2‡ | 3 | 4 | 5 | |
| Speckles | 2 (5.3) | 4 (5.2) | 2 (2.4) | 0 | 8 |
| Spots | 8 (21.1) | 18 (23.4) | 11 (13.1) | 0 | 37 |
| Scribbles | 5 (13.2) | 19 (24.7) | 22 (26.2) | 8 (25.8) | 54 |
| Blotches | 23 (60.5) | 36 (46.8) | 49 (58.3) | 23 (74.2) | 131 |
| Totals | 38 | 77 | 84 | 31 | 230 |

* Values in parentheses are percentages for each ground colour.
† Combining speckles and spots to increase expected frequencies, chi$^2$ = 16.1, df 6, $P < 0.02$.
‡ Very few eggs were classified as class 1 (very pale green) and therefore classes 1 and 2 were combined.

**Table 54**
Distribution of ground colour classes at three different areas of the east cliffs in 1977 (see Table 53 for details of colour code classes)

| Colour class | Area* | | | Total |
|---|---|---|---|---|
| | A | E | S | |
| 1 | 0 | 4 (4) | 1 (1) | 5 |
| 2 | 3 (14) | 17 (15) | 17 (15) | 37 |
| 3 | 7 (32) | 34 (31) | 37 (32) | 78 |
| 4 | 10 (45) | 41 (37) | 42 (37) | 93 |
| 5 | 2 (11) | 15 (13) | 17 (15) | 34 |
| Totals | 22 | 111 | 114 | 247 |

* Values in parentheses are percentages for each area.

markings, black markings being associated with dark ground colour. The frequencies of different ground colours did not differ among plots at A, E, and S (Table 54).

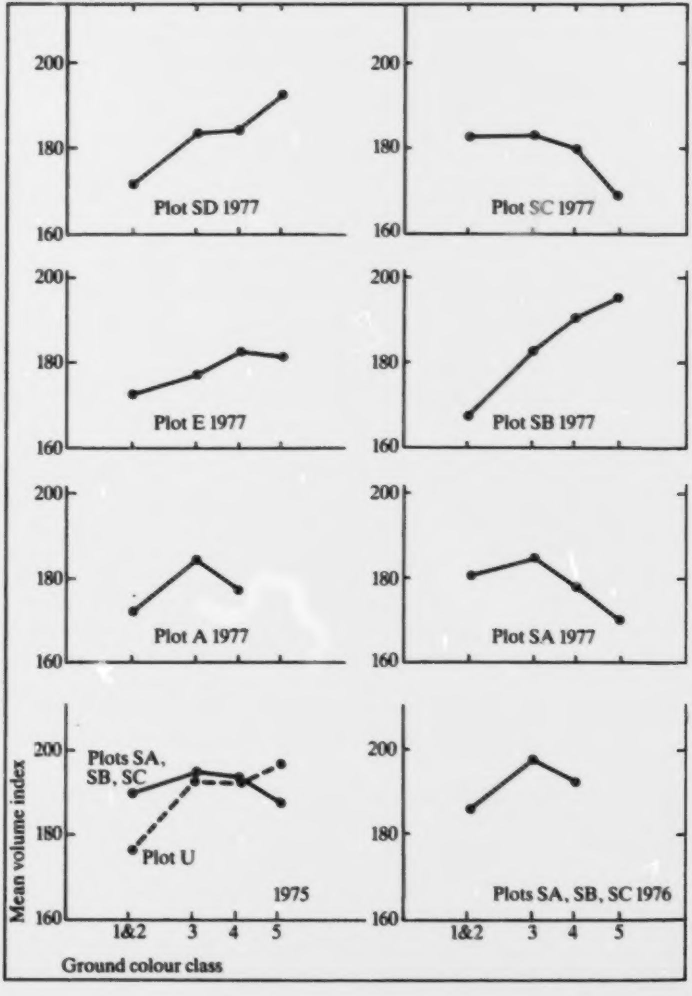
The volume of eggs was related in a complex manner to ground colour (Fig. 74). Ground colour categories may not be strictly comparable from year to year, but for plots SA, SB, and SC in 1975 and 1976, and for plots SA and SC in 1977, eggs that were intermediate in colour (class 3) were the largest, and darker (classes 4 and 5) or lighter (classes 1 and 2) eggs were smaller. In 1975 and 1977 the size of light and dark eggs varied more among plots than did the size of eggs of intermediate colour. Plots fell into two types: those where volume increased with ground colour density up to the darkest category (plots SB, SD, U) and those where eggs of intermediate colour were larger than either the darkest or lightest categories (plots A, SA, SC). Plots at E were similar to one another and fell between the two patterns described. The situation is very difficult to interpret, but dark eggs (class 5) apparently vary much more in volume than do lighter eggs and this accounts for at least part of the observed variation in ground colour/volume relationships. The variance of volume indices for class 5 eggs was significantly greater than that for class 4 eggs in 1977 (variance ratio = 2.86, $P < 0.01$), which was itself larger than the variances for the other three classes.

Although the distribution of ground colour classes was similar when areas containing relatively large numbers (> 20) of eggs were compared, on a smaller scale, eggs of similar colour and markings tended to be laid adjacent to one another, particularly on fairly isolated ledges. Plot UA, consisting of a single ledge, was occupied by four pairs in all 3 years, all of which laid eggs of class 1 or 2, with a ring of heavy black blotches at the large end. On the adjacent ledge, UB, where three to six eggs were laid each year, no eggs paler than class 3 were seen. At plot A in 1977, three of four eggs on one ledge were of an unusual type, class 4 in ground colour, but with heavy brown smudges with indefinite edges. Other eggs at plot A showed the normal colour variation.

### 2.4. Discussion

The difference in the weight and volume of eggs between 1977 and the preceding seasons presumably reflects differences in conditions during the pre-laying period. The much greater spread of egg-laying dates recorded in 1977 suggests a late season in which there was an interaction between the intrinsic mechanism controlling the timing of egg laying and environmental conditions determining the ability of females to lay at the optimum time. A positive correlation was found in this season between the dates of hatching and the initial weights of chicks (see this chapter, section 3.4). This possibly indicates a trade-off between egg size and date of laying, with some females producing smaller eggs than normal in order to lay as closely as possible to the usual date and others holding back until a normal-sized egg can be produced. A similar mechanism was postulated by Perrins (1970) to account for conflicting trends in clutch size and egg weight for Great

**Figure 74**
Volume indices of eggs in relation to ground colour classes (classes 1 and 2 are combined). See text for details



Tits *Parus major*. In the exceptionally late season of 1978, egg volumes were even lower than in 1977, although the difference was not significant (Nettleship *et al*. 1980*b*). In 1979, however, Birkhead and Nettleship (1981*b*) found that Thick-billed Murre chicks hatching from larger eggs at Coburg Island and Cape Hay grew faster and fledged at greater weights than chicks from smaller eggs.

Variations in volume index in relation to ground colour suggest that colour polymorphism may be linked to other characters, including those determining egg volume. However, volume is more likely to be influenced by environmental factors than colour. The occurrence of small groups of eggs with similar unusual patterns of colour and markings raises the possibility that birds laying close together may be genetically related more closely than would be predicted by a model assuming random breeding-site selection within the colony. Evidence from other studies suggests that young Common Murres tend to return to breed close to the site where they were reared (Southern and Reeve 1941, Birkhead 1977*a*) and this, particularly if it applied to females, would explain the observed clumping.

# 3. Chick growth

## 3.1. Methods

To obtain hatching dates for chicks used in growth studies, we visited study plots daily in 1975, but only every 2 days in 1976 and 1977, to reduce disturbance. If an egg was pipping at one visit and hatched at the next we recorded it as having hatched the previous day, unless the chick was wet, in which case the egg was recorded as having hatched the same day, as were chicks hatched from eggs that had not been pipping on the previous visit. Practically all eggs found pipping hatched within 2 days, although a few (5%) took longer. Bad weather caused some irregularity in the schedule of visits.

All plots were visited between 1300 and 1900 h. In 1975 and 1976, after most chicks had hatched, visits were made every 3 days, but in 1977 the frequency of examination was increased to every 2 days. Mortality of chicks due to our visits was highest during the first 5 days after hatching, probably because chicks rapidly chill at this age when left unattended. Frequent visits when most of the chicks were more than 5 days old caused little mortality, although a few chicks panicked and fell off the ledge in response to the investigator's presence and the absence of their parents.

All chicks were measured at each visit for (1) body weight, determined to the nearest 1 g using a 300 g Pesola balance, and (2) length of the primary coverts, measured from the carpus to the tip of the longest covert, with the feathers flattened along a metal rule to give a maximum reading. These data were considered sufficient to monitor growth accurately (O'Connor 1978). Chicks were identified by a binary code of toe-nail clipping until they were old enough to be banded. Seven chicks of unknown age were measured at the North Spit colony on 11 August 1976 and their age estimated from the length of their primary coverts so that their weights could be compared with those measured on the east cliffs.

## 3.2. Plumage development

Hatching took between 1 and 3 days from the first pipping of the eggshell to the complete emergence of the chick. The chick made its first "pip" near the centre of the large end of the egg and then worked its way around in a circle, so that a cap was cut off at the large end. In several cases incubating adults were seen to peck at the margins of the hole and this behaviour may assist the emergence of the chick. The newly-hatched chick is covered in down, varying from pale brown, often with a rufous tint, to more or less black. Pale chicks often show some mottling on the head, especially the crown.

Feathers begin to develop immediately and down is almost completely replaced by feathers at 16 days, although some usually adheres around the head (Plate 18). Juvenile plumage is of two types: (1) resembling the summer plumage of the adult, with a black chin and throat, and (2) similar to the adult winter plumage, with white extending up to the base of the bill and to a line running below the eye. Intermediates also occur, but the majority of chicks can be readily classified as having "winter" or "summer" plumage.

**Table 55**
Proportion of chicks on two plots with "summer" and "winter" plumage in 1977 (see text for description of plumage types)*

| | Chick plumage | |
|---|---|---|
| Plots | Winter | Summer |
| E | 2 (5%) | 41 (95%) |
| S | 11 (23%) | 37 (77%) |
| Totals | 13 (14%) | 78 (86%) |

* $Chi^2 = 6.18$, df 1, $P < 0.02$.

A similar plumage dimorphism occurs in Razorbill chicks (P. Hudson, pers. commun.).

The proportions of winter and summer plumages differed significantly between the weighing plots at E and S (Table 55), but no differences were found in the timing of hatching or in any growth parameters. Harris (1973) noted polymorphism among the chicks of the Waved Albatross *Diomedea irrorata* and found that the different types were not uniformly distributed among sub-colonies, while Southern (1966) and Birkhead *et al.* (1980) observed that the distribution of the "bridled" variety of the Common Murre tended to be clumped within colonies. All of these observations suggest the presence of genetic differences between different sub-populations of large seabird colonies, a conclusion also indicated by the distribution of different colours and patterns of eggs.

The primary coverts, which form the gliding surface during the chick's descent from the cliffs, begin to develop as soon as the chick hatches and the quills burst at 6 to 8 days after hatching. They lengthen slowly at first, but spurt at 10–11 days of age, after the feathers are fully emerged from the quills. The growth rate then remains steady until ca. 18–19 days, when it begins to decrease gradually, but the feathers continue to grow at least until day 24, so that the length of the primary coverts at fledging, unlike the weight at fledging, is closely correlated with the age of the chick. The continuous growth of the covert feathers throughout the chick-rearing period makes this measurement more suitable than weight for determining the age of chicks.

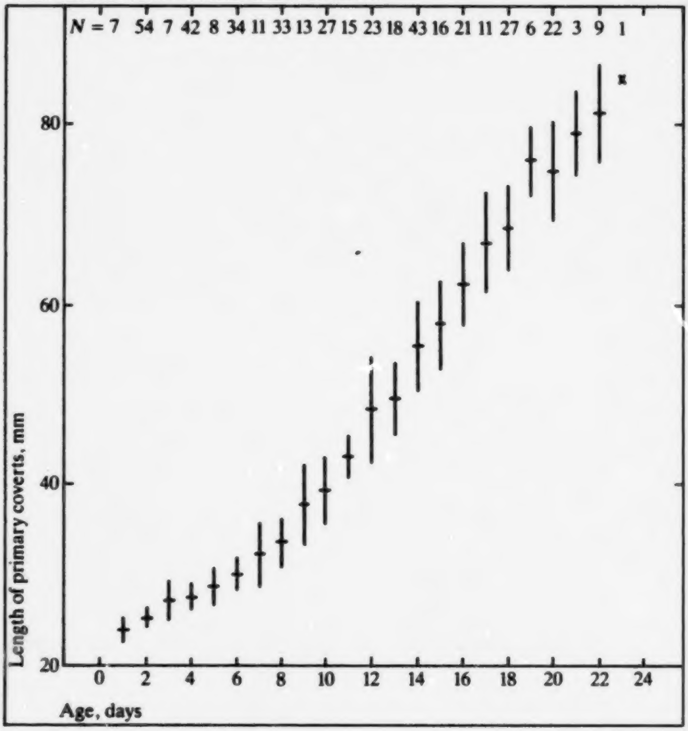
The pattern of development of the covert feathers was very similar in all 3 years and is shown for 1977 in Figure 75.

### 3.3. Weight

Parents began to feed chicks as soon as the eggs had hatched. Birds sometimes brought fish back to the site before the egg had hatched, presumably in response to the calls of the chick, which began once the shell had been pipped. These fish were often deposited beside the egg, but it is not known whether they were eaten later by the adults themselves or by the chicks after hatching. We observed chicks being fed within a few hours of hatching, consequently at Prince Leopold Island chick weight increased from the first day. This differs from the observations of Tuck (1961) and Uspenski (1956), who both found that chicks lost weight during the first and second days, but agrees with those of T.R. Birkhead (pers. commun.) on the Common Murre.

The weight increases recorded for individual chicks varied considerably between visits, particularly during the second half of the

**Figure 75**
Mean length of primary coverts in relation to age for chicks measured at plot S in 1977. Vertical bars are one standard deviation



chick-rearing period. Increases were generally more constant in 1977 than in the preceding 2 years, however (Figs. 76 and 77). Part of the observed fluctuations may depend on how recently the chicks had been fed, but P.J. Hudson (pers. commun.) found that, in Atlantic Puffins, regular fluctuations in weight gain occurred even in captive birds fed at a constant rate. Some of the variation in weight increases may therefore be due to intrinsic developmental processes. To produce an average growth curve, weights for days on which chicks were not weighed were estimated by linear interpolation according to the method described by Hussel (1972). This had the effect of smoothing the curve compared to means based on the data alone (Fig. 78).

Smoothed growth curves of weight increase based on measurements at plots SA, SB, and SC illustrate differences in the pattern of weight increase between the three seasons (Fig. 79). The initial rate of increase over the first 8 days was similar in all years, although slightly higher in 1977; a sharp drop in the rate of increase occurred in all 3 years between 7 and 9 days after hatching. This inflection in the rate of growth can be seen most clearly if increases are plotted separately

**Table 56**

Inter-year comparisons for chick growth characteristics. Only chicks weighed on plots SA, SB, and SC are included (complete growth data are given in App. 22)

| Item | 1975 | 1976 | 1977 |
|---|---|---|---|
| Mean weight (g) at day 2 | 72.3 | 72.2 | 70.8 |
| SD | 5.64 | 8.03 | 9.03 |
| Range | 65–84 | 54–83 | 54–91 |
| Mean weight (g) at day 14[*] | 186.6 | 174.1 | 199.7 |
| SD | 25.92 | 20.78 | 29.09 |
| Range | 147–258 | 139–216 | 128–253 |
| Mean maximum weight (g)[†] | 204.4 | 211.6 | 221.5 |
| SD | 21.83 | 18.59 | 28.58 |
| Range | 179–258 | 183–251 | 171–272 |
| Mean weight (g) at fledging | 200.3 | 209.2 | 215.8 |
| Mean covert length (mm) at day 14 | 54.2 | 52.8 | 55.8 |
| Mean covert length (mm) at fledging | 71.8 | 76.1 | 73.5 |
| Median date of hatching (1 June = day 1) | 58.3 | 55.7 | 63.3 |
| Age at fledging (days) | 19.7 | 21.6 | 19.0 |
| *N* | 18 | 28 | 25 |

[*] Single classification ANOVA for weight at day 14, $F = 6.87$, $P < 0.001$.
[†] For maximum weight, $F = 0.794$, $P > 0.1$.

rather than cumulatively (Fig. 80). In 1975 and 1977 another inflection occurred at about 15 days, but not in 1976, when weight increase continued at about the same rate to beyond day 21.

The inflection which occurred at day 15 in 1975 was sharper for individual birds than the smoothed curve suggests and this becomes clear when cohorts are plotted separately (Fig. 81). Weight increase after day 16 was negligible for most chicks. Similarly, in 1977, plotting early- and late-hatched chicks separately shows that while early chicks continued to increase in weight rapidly until day 20, the growth curve for late chicks flattened out after day 18 (Fig. 82). In 1976, however, the growth curves of different cohorts were similar (Fig. 83).

Rates of weight increase were higher in 1975 than in 1976 during the first 13 days and lower thereafter. However, peak rates of weight increase occurred between days 6 and 8 in all 3 years. In 1976 and 1977 there was a considerable increase in the variability of weight increases among chicks at 8–10 days of age, when the first inflection in the growth curve occurred (Fig. 80). This suggests variability in the age at which the rate of weight increase slows down, which is probably related to intrinsic developmental factors.

Mean maximum weights were highest in 1977 and lowest in 1975, although heterogeneity among years was not significant (Table 56). Weights at day 14 differed significantly between years, however, being highest in 1977 and lowest in 1976. Lack of significant heterogeneity between maximum weights is probably related to compensatory differences in the length of the chick-rearing period. This analysis includes only measurements made at plots SA, SB, and SC. Evidence for variation in maximum weights between different parts of the colony was obtained in 1976 from seven chicks weighed at the North Spit colony on sites ca. 20 m above sea level. The ages of these chicks ranged from 15 to 25 days (mean = 19.25). Their mean weight of 229.0 g was significantly heavier than the mean maximum weight of chicks weighed at the East Cliff colony ($t = 4.27$, df 36, $P < 0.01$) and all

**Figure 76**
Growth curves for five chicks selected at random from those weighed on sites at plot S in 1976

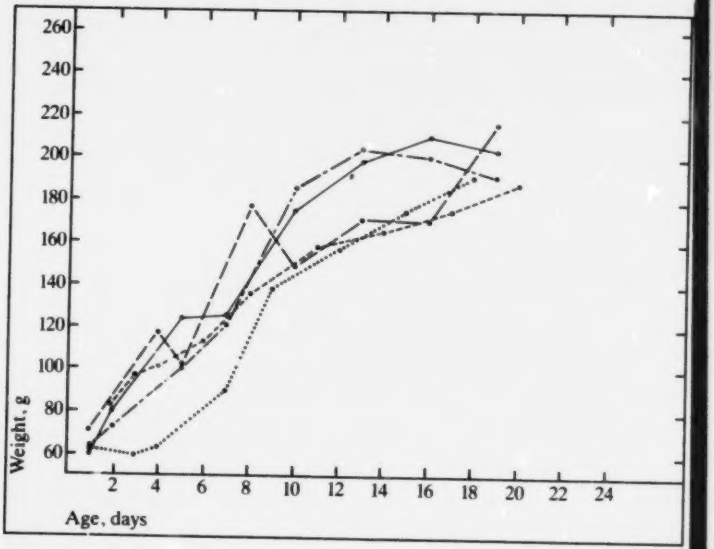


**Figure 77**
Growth curves for five chicks selected at random from those weighed on sites at plot S in 1977 (the same random numbers selected for the 1976 sample were used for the 1977 sample)

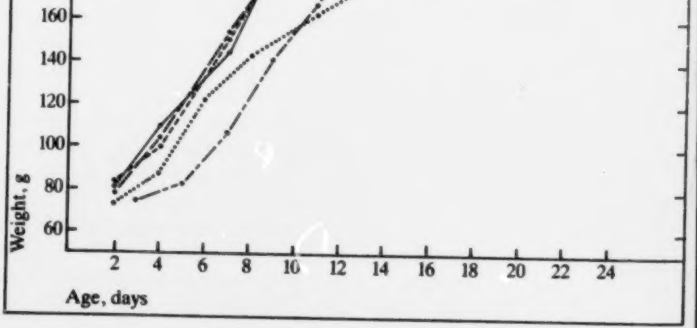


**Figure 78**
Mean weights of chicks measured in 1976 in relation to age and smoothed growth curve for the same sample using linear interpolation to estimate weights on days when measurements were not taken

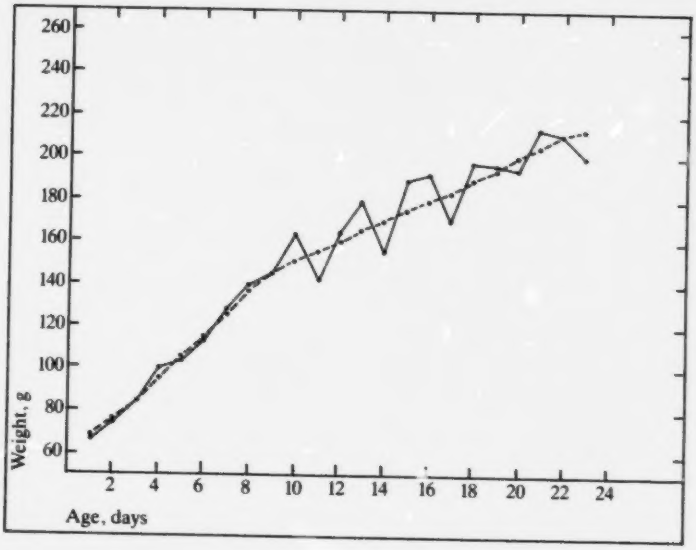


**Figure 79**
Smoothed growth curves for all chicks weighed on plots SA, SB, and SC combined in 1975, 1976, and 1977

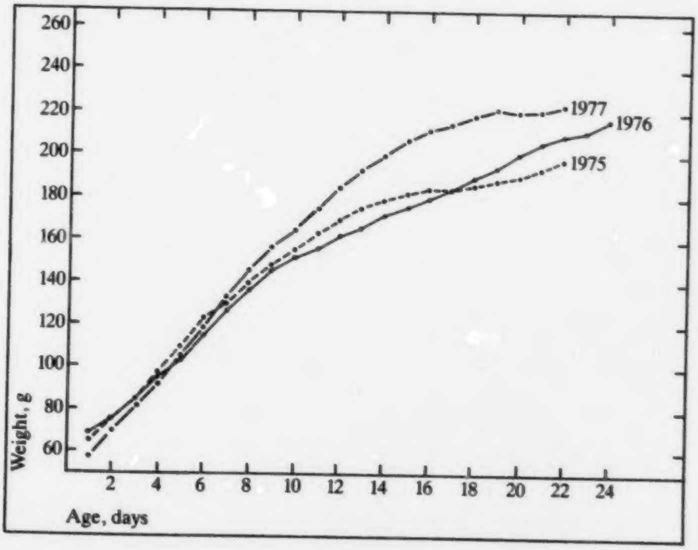


**Figure 80**
Mean daily weight increments of chicks weighed on plots SA, SB, and SC combined in 1975, 1976, and 1977 and standard deviations of the increments

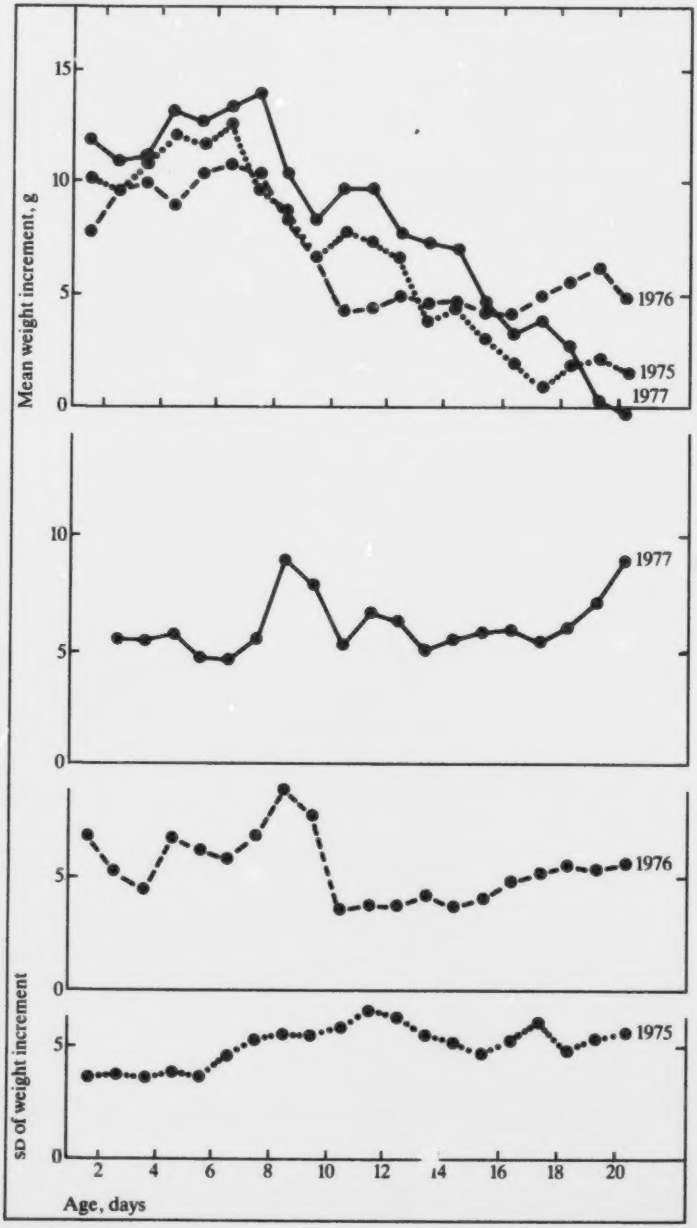


**Table 57**
Inter-plot comparisons for chicks weighed on plots at E and S (SA–SD) in 1977

| | Plot E | | Plot S | | |
|---|---|---|---|---|---|
| Item | Mean | SD | Mean | SD | *t* |
| Weight (g) at day 2 | 70.76 | 7.73 | 69.41 | 8.47 | 0.36 |
| Weight (g) at day 14 | 181.50 | 18.66 | 204.51 | 25.17 | 4.34* |
| Maximum weight (g) | 212.62 | 22.73 | 230.95 | 27.35 | 3.06* |
| Fledging weight (g) | 209.79 | 21.93 | 225.41 | 28.11 | 2.59* |
| Covert length (mm) at day 14 | 52.91 | 3.71 | 55.59 | 5.33 | 2.22 |
| Covert length (mm) at fledging | 70.94 | 6.95 | 75.05 | 7.53 | 2.38† |
| Median date of hatching (1June = day 1) | 63.26 | 5.03 | 62.35 | 4.88 | 0.77 |
| Age at fledging (days) | 19.47 | 2.06 | 19.38 | 2.44 | 0.17 |
| *N* | 34 | | 37 | | |

* $P < 0.01$.
† $P < 0.05$.

were well above the weight predicted for their age by the smoothed growth curves for that year (Fig. 83).

In 1977 growth rates of chicks on plots at E (EA, EB, EC) significantly differed from those at S (SA, SB, SC, SD) (Fig. 84). Initial weight increases, up to day 10, were similar, but the change in the rate of increase after day 10 was much greater at E than at S, so that mean weights at day 14 were already significantly different ($t = 4.34$, df 69, $P < 0.001$), as were maximum weights ($t = 3.06$, df 69, $P < 0.01$). Weight varied considerably more from day 10 onwards at S than at E. Primary coverts were significantly longer at S than at E, both at day 14 and at fledging. Egg volume did not differ significantly, although the larger sample measured initially (including eggs from which the chicks were not weighed) suggested that eggs at E may have been smaller on average than those at S (see Table 52). Neither initial weight (day 2) nor covert length (Table 57) differed significantly.

### 3.4. **Maternal influence**

Certain aspects of chick growth are apparently influenced by the state of the female during the pre-laying period, via the twin effects of egg size and date of laying. To examine these influences we prepared a correlation matrix for the parameters listed in Table 56. We used the weight of chicks on day 2 as a measure of initial weight, in preference to weight on day 1, because the latter could not be estimated by linear interpolation and because more direct weighings were available for day 2 chicks. We used weight and covert length at day 14 as measures of growth rate and all chicks included in the analysis survived to this age. Prior to the analysis we predicted the following correlations:

(1) initial weight would be negatively correlated with date of hatching,
(2) weight and covert length at day 14 would be positively correlated with initial weight,
(3) weight and covert length at day 14 would be negatively correlated with date of hatching,
(4) age at fledging would be negatively correlated with the date of hatching (Chapter III, section 2.1) and
(5) age at fledging would be negatively correlated with weight and covert length at day 14.

**Figure 81**
Smoothed growth curves for two cohorts of chicks weighed on sites at plot S in 1975: (*a*) Chicks hatched 26–28 July; and (*b*) chicks hatched 29–30 July. Arrows indicate points of inflection

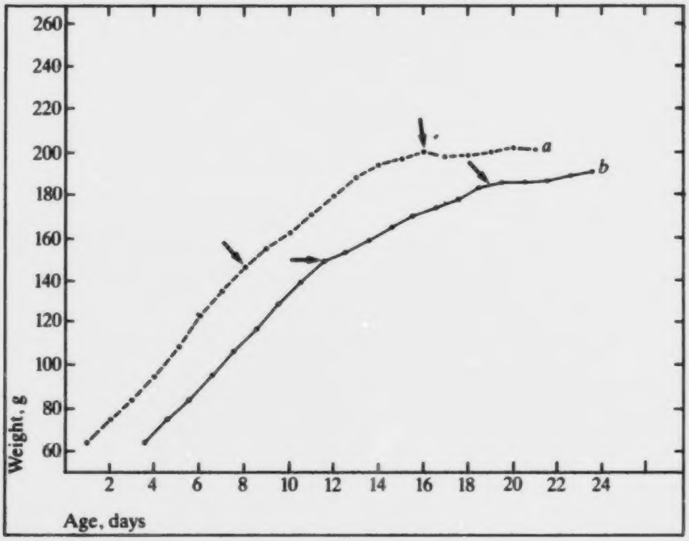


**Figure 82**
Smoothed growth curves for early chicks (hatched before 29 July) and late chicks (hatched after 6 August) weighed on sites at plot S in 1977: (*a*) Chicks hatched before 29 July; and (*b*) chicks hatched after 6 August. Arrows indicate points of inflection

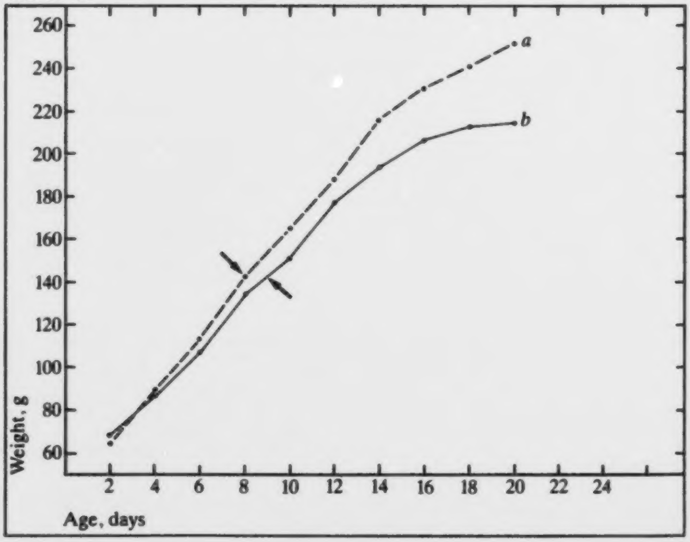


**Figure 83**
Smoothed growth curves for two cohorts of chicks weighed on sites at plot S in 1976: (*a*) Chicks hatched 23–25 July; and (*b*) chicks hatched 26–28 July. Arrows indicate points of inflection, and dots represent individual chicks weighed at the north spit colony on 11 August 1976 (ages are estimated from the length of primary coverts)

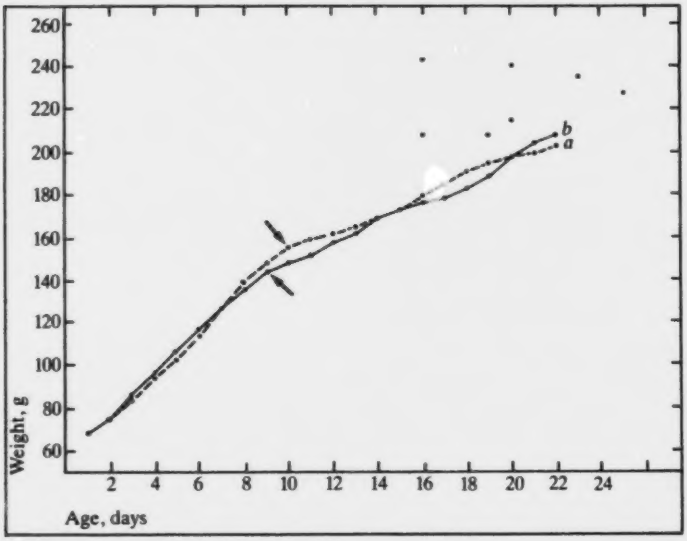
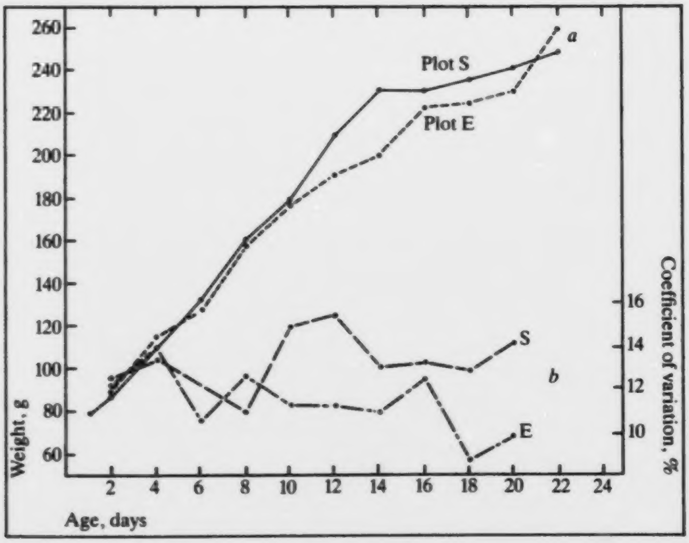


**Figure 84**
Growth curves for chicks weighed in 1977 on sites at plots E and S (*a*), and coefficients of variation (*b*). No interpolated figures are included



The length of the fledging period was equated with the age of the chick at its last weighing. Because most chicks fledged during the night, fledging periods used here may be up to 36 h shorter than actual fledging periods.

Predictions 1–4 were based on the assumption that birds laying early are either more experienced or better in quality than those laying late. Thus, they are capable of laying larger eggs and maintaining a higher rate of feeding, allowing their chicks to increase in weight and grow their feathers more rapidly than late-hatching chicks. Studies of other seabirds have shown that the size of eggs declines with date of laying (Coulson 1963, Nelson 1966, Parsons 1975, Ashcroft 1976, Brooke 1978, Lloyd 1979). Prediction 5 is based on the additional assumption that the condition of the chick is one of the factors determining its age at fledging, and that chicks that grow quickly will fledge earlier than those growing more slowly.

Analysis of data from plots at S in 1977 gave the predicted correlations except for prediction 1: initial weight had a significant positive correlation with date of hatching ($P < 0.05$) instead of the predicted negative relationship (Table 58). All the other correlations were significant ($P < 0.05$) when inter-correlations were controlled by partial correlation, except for the correlation between age at fledging and weight at day 14 (prediction 5), which was as predicted but insignificant. For the plots at E, date of hatching was not correlated to initial weight, covert length, or weight at day 14. No significant correlations were found between covert length or weight at day 14 and age at fledging, but both day 14 measurements were significantly correlated with initial weight. The predicted negative correlation between age at fledging and date of hatching was also found (Table 59).

The 1975 and 1976 samples were smaller than the two 1977 samples and not many correlations were significant, though predictions 1, 4, and 5 were consistently supported. A summary of results in all 3 years in relation to the initial predictions is given in Table 60. Evidence from all four sets of data suggests that the predicted negative correlation between initial weight and date of hatching is not a regular feature of the Prince Leopold Island colony, but that the other predictions are correct. Furthermore, all data show positive correlations between weight at day 14 and both the maximum weight attained and the weight at fledging. Thus, chicks that reach high weights during the first 14 days of life maintain their lead and slower growing chicks do not catch up. The consistent positive correlations between covert length and weight at day 14 show that chicks increasing in weight rapidly are also growing their feathers faster than those increasing in weight more slowly. There is no trade-off between feather growth and weight increase.

Weight increases in the last 2 days before fledging were lower than increases for chicks of the same age that fledged later (Table 61). The observed differences are not significant when taken for each age category individually, but the fact that the comparison for chicks last weighed at 21 days approaches significance ($P \simeq 0.07$) and that the results are largely consistent suggests that the tendency is probably real.

**Table 58**
Correlation matrix for growth characteristics of chicks (listed in Table 56) on study plots at S in 1977 ($N = 37$). Coefficients in brackets are given as partial coefficients below*

| Item | Age at fledging | Mean weight |  |  |  | Mean covert length |  |
|---|---|---|---|---|---|---|---|
|  |  | Day 2 | Day 14 | Maximum | Fledging | Day 14 | Fledging |
| Date of hatching | −0.284† | 0.357† | (−0.145) | −0.310† | −0.251 | (−0.101) | −0.352† |
| Age at fledging |  | −0.377† | (−0.046) | 0.378† | 0.291† | −0.415‡ | 0.792‡ |
| Weight, day 2 |  |  | 0.277† | 0.041 | 0.119 | 0.693‡ | −0.048 |
| Weight, day 14 |  |  |  | 0.796‡ | 0.739‡ | 0.488‡ | 0.230 |
| Weight, maximum |  |  |  |  | 0.938‡ | 0.213 | 0.567‡ |
| Weight at fledging |  |  |  |  |  | 0.259 | 0.470‡ |
| Coverts, day 14 |  |  |  |  |  |  | 0.077 |

* Partial correlation coefficients: Weight at day 14 in relation to date of hatching, controlling for weight at day 2: $r$ (partial) = −0.272 ($P \simeq 0.05$);
Covert length at day 14 in relation to date of hatching, controlling for weight at day 2: $r$ (partial) = −0.518‡;
Age at fledging in relation to weight at day 14, controlling for date of hatching: $r$ (partial) = −0.077.
† $P < 0.05$.
‡ $P < 0.01$.

**Table 59**
Correlation matrix for growth characteristics of chicks (listed in Table 57) on study plots at E in 1977 ($N = 34$)

| Item | Age at fledging | Mean weight |  |  |  | Mean covert length |  |
|---|---|---|---|---|---|---|---|
|  |  | Day 2 | Day 14 | Maximum | Fledging | Day 14 | Fledging |
| Date of hatching | −0.462† | 0.054 | 0.053 | −0.058 | 0.003 | 0.050 | −0.288* |
| Age at fledging |  | −0.074 | −0.150 | 0.143 | 0.176 | 0.021 | 0.791† |
| Weight, day 2 |  |  | 0.279* | 0.287* | 0.210 | 0.346* | 0.176 |
| Weight, day 14 |  |  |  | 0.732† | 0.603† | 0.662† | 0.214 |
| Weight, maximum |  |  |  |  | 0.950† | 0.544† | 0.454† |
| Weight at fledging |  |  |  |  |  | 0.411† | 0.416† |
| Coverts, day 14 |  |  |  |  |  |  | 0.479† |

* $P < 0.05$.
† $P < 0.01$.

**Table 60**
Summary of correlations among growth parameters of chicks on study plots S and E in relation to predictions for all years. Coefficients in brackets are the partial correlation coefficients given in Table 58

| Parameters | Predicted correlations | Plot S 1975 ($N = 19$) | Plot S 1976 ($N = 28$) | Plot S 1977 ($N = 37$) | Plot E 1977 ($N = 34$) |
|---|---|---|---|---|---|
| (1) Weight at day 2 |  |  |  |  |  |
| vs. weight at day 14 | + | +0.267 | +0.170 | +0.277* | +0.279* |
| vs. covert length, day 14 | + | 0.000 | +0.511* | +0.693† | +0.346† |
| (2) Weight at day 2 vs. date of hatching | − | −0.162 | +0.073 | +0.357* | +0.054 |
| (3) Date of hatching |  |  |  |  |  |
| vs. weight at day 14 | − | −0.330 | +0.032 | (−0.272)* | +0.053 |
| vs. covert length, day 14 | − | −0.586* | +0.157 | (−0.518)† | +0.050 |
| (4) Date of hatching vs. age at fledging | − | −0.216 | −0.183 | −0.377* | −0.462† |
| (5) Age at fledging |  |  |  |  |  |
| vs. weight at day 14 | − | −0.341 | −0.492* | (−0.077) | −0.150 |
| vs. covert length, day 14 | − | −0.407 | −0.449* | −0.415† | +0.021 |

* $P < 0.05$.
† $P < 0.01$.

**Table 61**
Comparison of the weight change observed for chicks during their last 2 days before fledging with the change in weight of chicks at the same age which fledged later, on study plots at G and S combined for 1977 ($z$ obtained by calculating $U$ for the Mann-Whitney test; only direct measurements were included.)

| Age, days | Chicks fledging<br>Mean wt. change, g | $N$ | Chicks not fledging<br>Mean wt. change, g | $N$ | $z$ | $P$ |
|---|---|---|---|---|---|---|
| 17 | 3.00 | 5 | 9.55 | 9 | 0.77 | 0.23 |
| 18 | 3.62 | 13 | 7.11 | 19 | 0.63 | 0.26 |
| 19 | 9.75 | 4 | 9.67 | 9 | 0.1 | 0.5 |
| 20 | −0.30 | 23 | 1.00 | 7 | 0.66 | 0.25 |
| 21 | −7.20 | 5 | 1.08 | 12 | 1.48 | 0.07 |

### 3.5. Effects of weather

Both wind speed and sea conditions have been implicated in affecting the feeding success of marine fish-eating birds and, consequently, the rate at which they feed their chicks (Dunn 1973, Birkhead 1976*b*, Lloyd 1976). We could not, however, compare chick growth with sea conditions in our study, because most murres fed in the open water more than 30 km from the Prince Leopold Island colony (Nettleship and Gaston 1978), where sea conditions were probably different from those we observed around the island. Weather conditions that we observed at the colony, however, were probably similar to those over much of the birds' feeding range and we therefore examined the effect of weather on chick growth.

To do so, we calculated the median change in weight between each 2-day age class and the proportion of chicks exceeding this median change in weight over each 2-day period. In 1977 no correlation was found in the proportion of chicks exceeding the median weight increase at plots E and S ($r_s = 0.02$, $N = 16$, $P > 0.5$), nor were any correlations found for weights of chicks in either area with wind speed, barometric pressure, or visibility. On 19 August 1977, however, when wind speeds exceeded 50 km/h throughout the day, chicks at both areas experienced their lowest growth rates, with only 27% of chicks at S and 17% at E exceeding the median weight increase for their age class. Moreover, feeding rates recorded on 19 August were much lower than those recorded in the rest of the season (see this chapter, section 4.2).

In 1976 no correlation was found between wind speed and chick growth, but when days with winds of 48 km/h or more were compared with days when wind speeds were lower, the weight increases of chicks on days of high winds were significantly lower (Mann-Whitney $U = 14$, $z = 2.49$, $P < 0.01$). Tuck and Squires (1955) mention that at Akpatok Island in 1954 no food was brought to the colony at all on one day of very high winds during the chick-rearing period. Weather appears to have little effect on chick growth under normal conditions, therefore, but may depress growth rates during periods of exceptionally strong winds.

### 3.6. Discussion

The conditions under which the chick develops remain more or less unchanged from hatching to fledging; the chick is brooded almost continuously on the same spot and there is no sibling competition.

Consequently, measurements of growth illustrate very clearly the interaction between intrinsic developmental processes and the rate at which the chick is fed. The size of the egg is in turn determined by an interaction of intrinsic and environmental factors operating on the female prior to laying. The quality of the male may also be involved, because it may influence the type of breeding site obtained, which could affect the size of the egg and the date of laying through differences in microclimates (Chapter III, section 4.3).

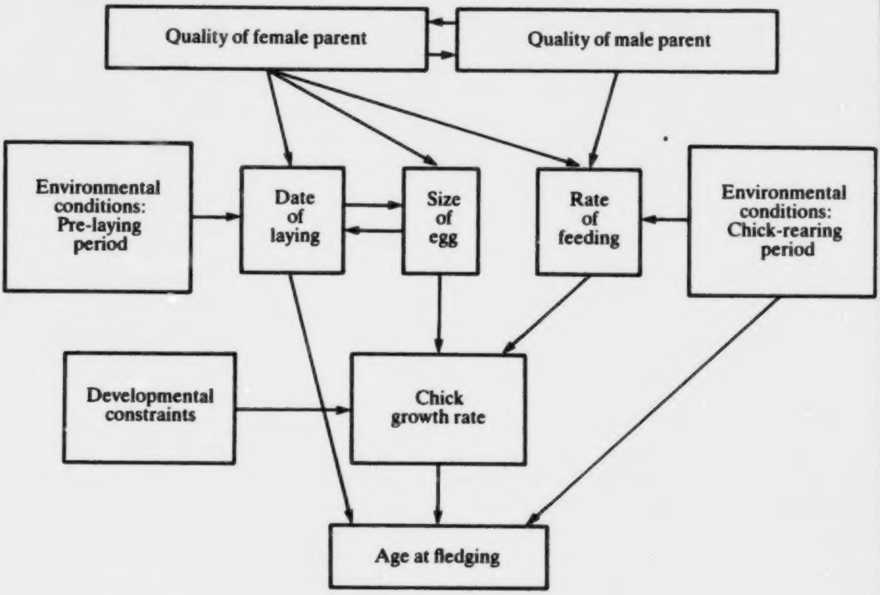
Age and breeding experience are strongly correlated with breeding success in several seabird species (Black-legged Kittiwake, Coulson and White 1958, 1961; Northern Gannet, Nelson 1966; Manx Shearwater, Brooke 1978) and are important determinants of parental quality. Pairs often remain together over several successive years, so that experienced breeders are likely to have experienced mates. In addition, if the process of selecting a mate involves competition, then pairing should be assortative for quality, even among birds of the same age, and such competition is likely to be strong in species where the same mate is retained from year to year (Zahavi 1975). The net result is that the quality of male and female parents is likely to be highly interdependent.

Environmental conditions prior to laying and the quality of the female, particularly her ability to find food, determine the size of the egg and the date of laying. These in turn influence the weight and covert length of the chick in relation to its age and hence affect its condition at fledging, which is probably crucial for immediate post-fledging survival. The provisioning ability of the parents also determines the state of the chick at fledging (Harris 1978). Figure 85 illustrates the probable interrelationship of intrinsic and extrinsic factors in determining chick growth and the length of the fledging period.

In 1975 and 1977 at plot S chicks that hatched early were heavier and had longer coverts at day 14 than those hatching later, the effect being more pronounced for the coverts. There was no evidence from observed feeding rates that early chicks received more food, but in any case Nettleship (1972) and Hudson (1979) have shown that for Atlantic Puffins the amount of food fed to chicks does not affect the rate of growth of the wing feathers. Harris (1966) produced similar evidence from twinning experiments on Manx Shearwaters. Because food was very abundant in 1977, the majority of chicks could probably sustain their maximum rates of growth and hence observed differences may have been caused by variability among chicks in their intrinsic rates of growth. It is not clear why this should have been related to dates of laying, but MacRoberts and MacRoberts (1972) found that incubation periods decreased with season in the Herring and Lesser Black-backed gulls. If this effect occurred in Thick-billed Murres, early chicks might hatch at a more advanced stage of development than late chicks. The effect of initial weight on weight at day 14 can be more readily explained by assuming that weight increments are proportional to starting weight.

The coverts continue to grow throughout the chick-rearing period while weight usually levels off. As a result, early chicks, which generally remain longer on the ledges than late chicks, tend to fledge with a lower ratio of weight to wing-area than late chicks, despite achieving higher maximum weights. Mortality caused by striking

**Figure 85**
The interaction of parental quality and environmental conditions in determining the growth rates and age at fledging of Thick-billed Murre chicks


Quality of female parent
Quality of male parent
Environmental conditions: Pre-laying period
Date of laying
Size of egg
Rate of feeding
Environmental conditions: Chick-rearing period
Developmental constraints
Chick growth rate
Age at fledging

lower ledges during the descent is high, at least at certain plots (Chapter III, section 3.2), suggesting that selection for optimum weight to wing-area ratio could be critical at this point, which might place a constraint on the rate of increase in the weight of late-hatching chicks.

Growth rates for chicks up to 8 days old are similar among the 3 years, which probably indicates that up to this age the adults could supply sufficient food to allow the chicks to grow at the maximum rate possible. The inflection in the growth curve at 7–9 days of age in all 3 years coincides with the development of the capacity to thermoregulate, which occurs at 6–8 days (Rol'nik 1948, Johnson and West 1975) and presumably indicates an increase in metabolic activity at this age. The contemporaneous increase in variability has been noted for Cassin's Auklet *Ptychoramphus aleuticus* (Manuwal 1972) and the Pigeon Guillemot *Cepphus columba* (Drent 1965) at a similar developmental stage.

Divergences from the maximum rate of weight increase at ages beyond 10 days probably indicate differences between the potential capacity of the chicks and the abilities of their parents to provision them. In 1977 early-hatched chicks continued to grow at close to the initial rate up to 14 days of age, suggesting that in this season conditions were favourable enough for them to maintain the maximum rate of growth for 4–5 days longer than usual. The flattening out of the growth curves of chicks weighed in 1975, however, suggests that provisioning rates in that season did not exceed the rate necessary to cover the metabolic requirements of the chicks after ca. 16 days. This supports the contention of Greenwood (1964), Sealy (1973*a*), and Birkhead (1977*b*) that the semi-precocial fledging of murre chicks is necessary, because their parents are unable to provision them rapidly enough for them to complete their development on the breeding site.

Although rates of provisioning remain the same, the rate of growth in weight decreases during the last 2 days before fledging, possibly because of increased physical activity by the chicks [e.g., wing flapping, (Sealy 1973*a*)], or lowering of the water content of their body tissues due to processes of maturation (Ricklefs 1968). The weight recession reported by some investigators for murre chicks just prior to fledging (Johnson 1944, Tuck 1961, Johnson and West 1975) is not a typical feature of the development of Thick-billed Murres on Prince Leopold Island, but may occur in years when food is scarce. Among early-hatched chicks in 1975, weight curves flattened out completely after day 15 and some decreased.

The age at which the chick fledges must be determined by a number of conflicting selection pressures. The danger of predation on the breeding site, and from rock falls, and the increasing difficulty experienced by the parents in providing the chick with sufficient food to sustain its development cause selection for a reduction in the length of the chick-rearing period. At the same time the demands of the long glide to the sea and the need for thermoregulation after fledging cause selection for an increase in the length of time spent on the cliff to maximize feather development. The chick cannot afford to commit all its resources to structural growth and has to lay down energy reserves to tide it over until it is self-supporting. The size of these reserves, in turn, has to be balanced against the need to optimize the weight to wing-area ratio at fledging.

Although it is obviously of the greatest importance to the chick to commit itself to fledging in the optimum condition for subsequent survival, observations of the timing of fledging in relation to weather conditions (Chapter III, section 2.4) suggest that, after achieving a certain threshold stage of development, the physical condition of the chick is largely subordinated to environmental factors in determining the timing of fledging. This may account for the rather poor correlations found between measurements of weight and covert length at day 14 and age at fledging, although the disturbance involved in taking the measurements may also have caused some chicks to fledge prematurely.

Another factor influencing the age at fledging, but unrelated to the physical condition of the chick, was the timing of fledging in the rest of the colony. The inverse correlation between date of hatching and age at fledging occurred because fledging was much more highly synchronized than laying, perhaps to reduce gull predation through the "swamping" effect of a large number of chicks leaving the cliffs at once (Kruuk 1964, Williams 1975). This meant that early-hatching chicks delayed their departure while those hatching late advanced it. The mechanism involved may well relate to some kind of social stimulation developing through the mass departure of huge numbers of chicks and the associated vocalizations.

The weight of chicks at fledging was correlated with their subsequent survival in a number of species of birds (Great Tit, Perrins 1965; House Sparrow *Passer domesticus*, Dawson 1972; Manx shearwater, Perrins *et al.* 1973; South African Gannet *Sula capensis*, Jarvis 1974). Although little is known about the survival of young murres during their first few weeks after fledging, the size of stored energy reserves might be crucial at this period, particularly if weather conditions reduce feeding efficiency. Birkhead and Hudson (1977) found that for Common Murres the rate of recovery of banded birds during their first year was highest immediately after fledging. Differences in mean fledging weights between years may, therefore, make a significant contribution to differences in the proportion of chicks surviving to maturity.

The considerable flexibility of growth rates, as measured by changes in weight, is almost certainly the result of differences in the availability and predictability of food among the 3 years of the study. Variability in growth rates from year to year and among different colonies appears to be typical of colonial alcids (Uspenski 1956, Kartaschew 1960, Nettleship 1972, Johnson and West 1975, Lloyd 1976, Ashcroft 1976, Harris and Hislop 1978). The mean fledging weights of Thick-billed Murre chicks recorded by different observers range from about 125 g (Uspenski 1956) to 260 g (Kaftanovskii 1951) or more than 100% of the minimum.

# 4. Feeding rates and chick diet

## 4.1. Methods

The rates at which parent birds deliver food to their chicks have been used previously to:

(1) estimate the food intake of the young (Tuck and Squires 1955)

(2) monitor changes in the rate of provisioning in relation to weather conditions (Birkhead 1976*b*), and

(3) estimate the foraging radius of the parent birds (Pearson 1968).

Watches to determine the rate at which Thick-billed Murre chicks on Prince Leopold Island were fed were undertaken regularly in all 3 years of the study.

In 1975 and 1976, we watched plot S1 every 5 days throughout the chick-rearing period to determine feeding rates. In 1975 each watch was maintained over 24 h, for alternate hours up to 8 August, and continuously on later watches. Because no significant circadian rhythm in the frequency of feeding visits was detected in 1975, watches in 1976 were reduced to 12 h between 0800 and 2000 h, although 24-h watches were carried out on 31 July and 21 August. In 1977 the frequency of watches was increased to once every 3 days and their duration reduced to 4 h, from 1400 to 1800 h; the increased frequency was designed to better detect the effect of weather conditions on feeding rates. Watches were performed simultaneously at plots S1 and U to obtain some indication of variation between different parts of the colony. In addition to the normal weather records made at camp, wind speed and visibility were estimated at the plot every 2 h throughout these watches. An attempt was also made to compare growth rates measured at S with feeding rates observed at plot S1, 20 m away.

The parent murres usually delivered a single item at each visit, normally a whole fish, although two items were very occasionally brought. The size of items delivered to chicks was measured by several methods. In all 3 years observers estimated the length of items by comparing them with the length of the adult's bill. Comparisons of estimates with the measurements of items collected from chicks suggested that observers habitually underestimated lengths by approximately 20%. We obtained food items from birds shot while flying towards the colony and picked up stray items from the breeding ledges while measuring chicks. We could shoot incoming birds only when strong head-winds forced them to fly low and these conditions prevailed for only a few days each season.

Every 3 days in 1977 a sample of 20 chicks was fitted with collars fashioned out of wire pipe-cleaners, which prevented the chicks from swallowing food. Collars were left on the chicks for approximately 4 h, after which time about 60% of the chicks had food in their gullets. A few fish were also found on the ledges, presumably because the chicks were unable to swallow them. The proportion of chicks found with food was approximately what would be expected on the basis of observed feeding rates, although the possibility that a few small items slipped through the collars cannot be ruled out.

Food specimens were provisionally identified in the field with final identification made later. Fish were measured from the tip of the rostrum to the fork of the tail and, if complete and fresh, were also weighed and preserved. Where the total body length of specimens could not be measured, the otoliths were removed and measured. Where the head was missing, the distance from the base to the tip of the tail was measured. The latter measurement was useful in the case of fish obtained from chicks fitted with collars, since partial digestion of the head had sometimes taken place before the fish was retrieved. For arctic cod *Boreogadus saida*, the most numerous species collected, the mean length of the otoliths was used to derive the body length from the formula given by Bradstreet (1977) and the length of the tail was used in the same way, employing a formula derived in the present study.

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**Figure 86**
Mean feeding rates to chicks observed during watches at plot S1 in 1975 and 1976 and at plots S1 and U combined in 1977

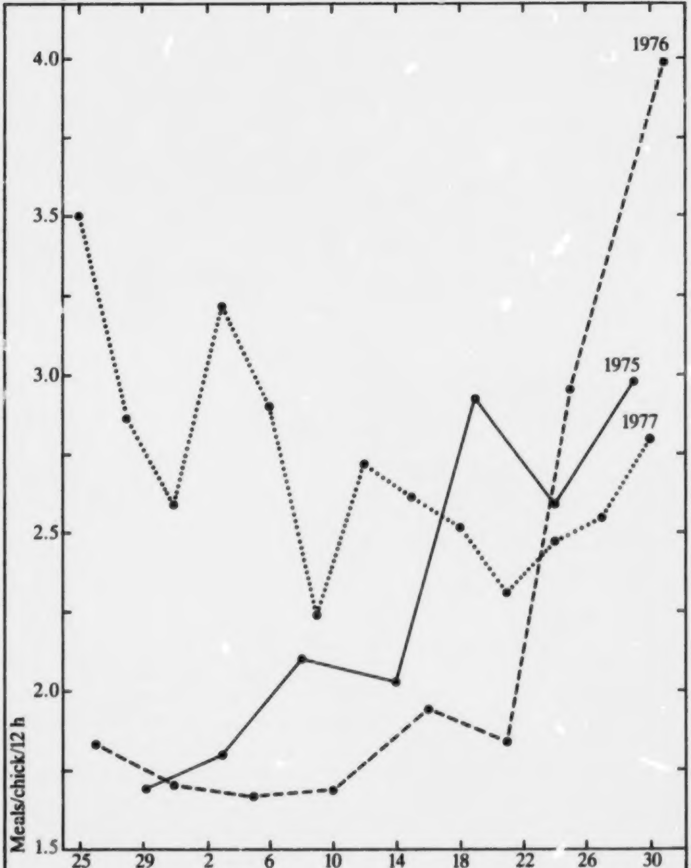
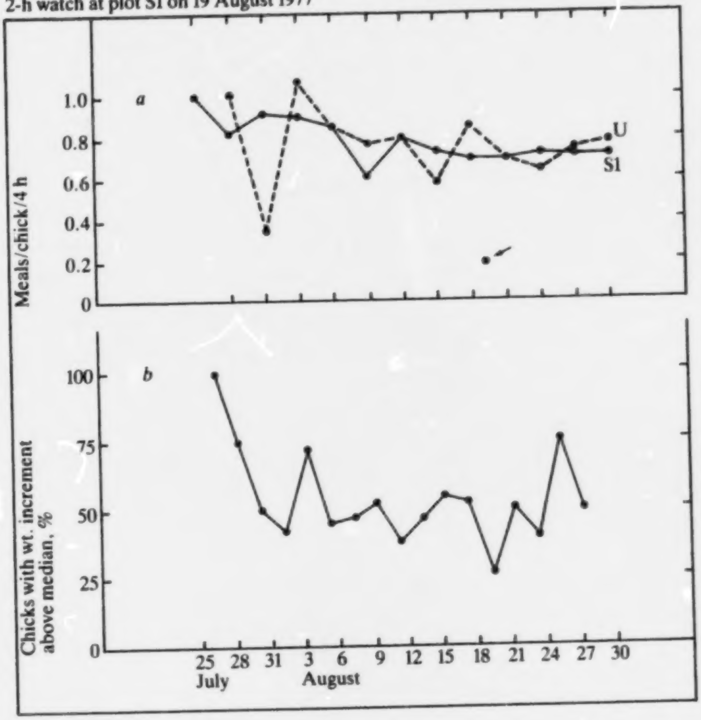


**Figure 87**
(*a*) Feeding rates to chicks observed during 4-h watches at plots S1 and U in 1977 and (*b*) percentage of chicks measured on sites at plot S which showed more than the median weight increase for their age class. Arrow on (*a*) indicates the result of a 2-h watch at plot S1 on 19 August 1977



## 4.2. Feeding rates

In 1975 and 1976 feeding rates increased from a mean of about 3.5 meals per day in late July to 6–8 meals by the end of August (Fig. 86). In 1977, however, date and feeding rate were negatively correlated, although this trend was reversed in late August. An analysis of feeding rates and weather conditions (wind speed, cloud cover, visibility, and barometric pressure) for 1977 revealed no statistically significant relationships, although the lowest feeding rate was recorded on 19 August, when wind speed was highest (> 56 km/h).

Rates of feeding observed simultaneously at S1 and U in 1977 did not differ significantly. Both showed a negative correlation with date, but there was no significant correlation between rates at the two plots (Fig. 87). On days when differences between the two plots were large, the variability among sites at S1 was also high.

To compare overall feeding rates throughout the entire chick-rearing period in 1977, we added the numbers of meals observed for individual chicks during the first five 4-h watches after they had hatched (Table 62). This included all the watches made before the chicks were 16 days old. Mean feeding rates during the first 16 days calculated in this way differed only slightly between plots S1 and U, but the distribution of feeding rates was different, being significantly bimodal at S1 (Fig. 88). At plot U the distribution of the number of meals delivered during the first 16 days approximated a Poisson distribution, as did the number of meals per chick observed on individual watches. The coefficient of dispersion (variance/mean) was nearly always less than one, however, suggesting that feeding visits were slightly more evenly spaced than the random intervals predicted by the Poisson model. A bimodal distribution of the number of meals delivered to chicks during their first 16 days (three watches) was also found at S1 in 1975, the effect being greater for chicks hatching during July than for those hatching later.

Figure 89 shows the location of chicks fed at above the median rate on plot S1 during their first 16 days, for both 1975 and 1977. The study plot is divided into three zones on the basis of physical characters: A, steep and north-facing; B, sloping and east-facing; and C, gently sloping and north-facing. Most of the sites in areas A and B were on narrow or broad, level ledges, while those in area C were mainly on platforms sloping towards the sea (Chapter III, section 4). A higher proportion of chicks in area A was fed at above the median rate than in areas B and C in both 1975 and 1977. In 1976 a higher proportion of chicks in area A was fed at above the median rate on 31 July, but the situation was reversed on 21 August (Table 63). A higher proportion of sites on area C were of the type associated with lower reproductive success [platforms, negative slope, no neighbours (Chapter III, section 4)] than on the other two areas. The low rates of feeding on area C may have been associated with a high proportion of young, inexperienced birds, or poor quality individuals. Because significant differences in feeding rates may occur between adjacent areas of the colony, caution is necessary in interpreting such observations, particularly in making inter-year or inter-colony comparisons.

No significant correlations were found at plot S1 in 1977 between the number of meals delivered to chicks during their first 16 days of life and their date of hatching or their age at fledging. At plot U,

**Table 62**
Distribution of numbers of meals delivered to chicks during the first five 4-h watches after hatching in 1977. Poisson and normal distributions calculated for the same means are also given*

| Study plot | | No. of meals/chick | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| Plot S1 | 3.76 | 3 | 6 | 14 | 33 | 12 | 27 | 11 | 5 | 0 | 0 |
| Poisson | | 2.6 | 9.8 | 18.34 | 22.9 | 21.5 | 16.2 | 10.1 | 5.4 | 2.6 | 1.6 |
| Normal | | 3.9 | 7.8 | 19.8 | 26.5 | 23.4 | 15.4 | 7.0 | 2.2 | 1.0 | 0 |
| Plot U | 3.94 | 0 | 1 | 6 | 10 | 8 | 5 | 2 | 1 | 1 | 1 |
| Poisson | | 0.8 | 3.1 | 5.8 | 7.2 | 6.8 | 5.1 | 3.2 | 1.7 | 0.8 | 0.3 |
| Normal | | 0.7 | 2.0 | 4.3 | 6.8 | 7.8 | 6.5 | 4.0 | 1.8 | 1.1 | 0 |

* Comparing distributions:
S1: observed vs. Poisson, $chi^2 = 20.08$, df 6, $P < 0.01$.
observed vs. normal, $chi^2 = 21.17$, df 6, $P < 0.01$.
(categories 0–1 and 7 and over were lumped to increase expected frequencies).
U: observed vs. Poisson, $chi^2 = 2.05$, df 6, $0.95 > P > 0.90$.
observed vs. normal, $chi^2 = 4.60$, df 6, $0.70 > P > 0.50$.
Comparing means, $t = 0.716$, $N = 146$, $0.5 > P > 0.4$.

**Table 63**
Proportion of chicks fed at above the median rate on three areas of study plot S1

| Watch | Median rate of feeding meals | % areas of plot S1* A | B | C | Chi$^2$ | *P* |
|---|---|---|---|---|---|---|
| 1975 (1st three 12-h watches) | 6 | 54 (56) | 27 (22) | 42 (36) | 4.53 | 0.05–0.1 |
| 1976 (31 July) | 3 | 54 (39) | 36 (11) | 17 (6) | 19.3 | <0.001† |
| 1976 (21 August) | 2 | 33 (27) | 25 (12) | 55 (29) | | |
| 1977 (1st five 4-h watches) | 5 | 47 (55) | 37 (24) | 24 (34) | 4.78 | 0.05–0.1 |
| 1975 and 77 (as above, combined)‡ | | 69 (65) | 40 (30) | 38 (47) | 12.82 | <0.01 |

* Values in parentheses are sample sizes.

† Proportions observed on 21 August were tested against expected frequencies based on the results obtained on 31 July.

‡ Proportions of sites where chicks were fed at above the median rate in at least 1 year, as a percentage of sites occupied at least once.

**Figure 88**
Distribution of numbers of meals delivered to chicks during (*a*) the first three 12-h watches after they had hatched in 1975, and (*b*) the first five 4-h watches in 1977. Broken line histograms show Poisson distributions calculated for the same means. Shaded histogram for 1975 shows chicks hatched in July only. Testing the observed distributions against the predicted Poisson distribution gives: 1977, chi$^2$ = 18.51, df 7, $P < 0.01$; 1975, chi$^2$ = 5.22, df 7, $P$ = 0.5–0.7; 1975 chicks hatched in July only, chi$^2$ = 10.21, df 7, $P$ = 0.1–0.2 (classes 0–2 and 9–10 are combined to increase frequencies)

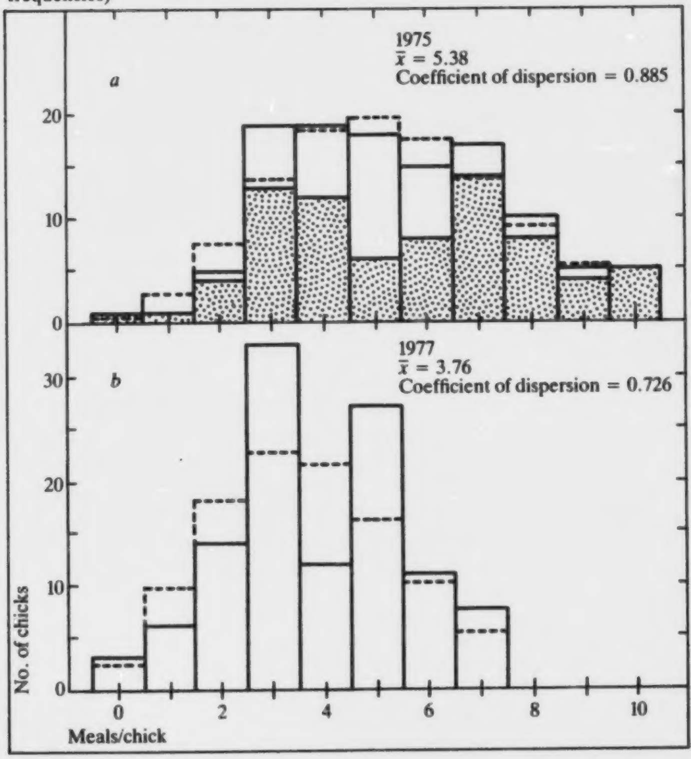
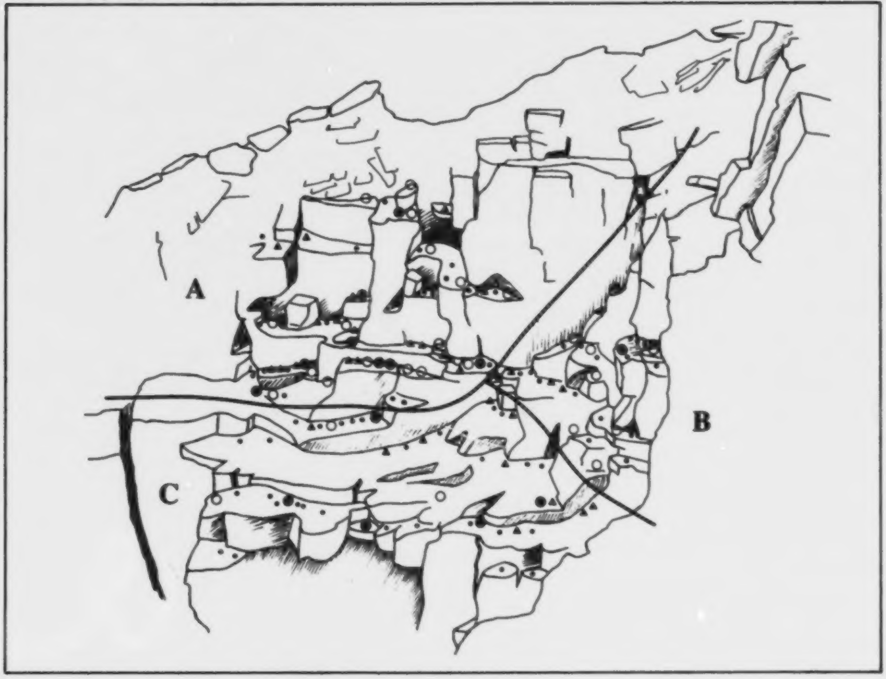


**Figure 89**
**Sketch of study plot S1 showing the position of chicks fed at above the median rate (1975 = 6 meals, 1977 = 5 meals) during the first three 12-h watches after they had hatched in 1975 (▲) and the first five 4-h watches in 1977 (○). The positions of chicks present in either year, but not fed at above the median rate, are indicated by a dot (•). Solid lines demarcate the three sub-areas of the plot (see text for details). (Drawn from study plot photo, App. 1)**



a small significant positive correlation was observed between the number of meals and the length of the chick-rearing period, probably the result of inter-correlations between date of hatching and age at fledging and between date and feeding rate.

No consistent variation in feeding rates in relation to the age of the chicks was observed (Fig. 90). In 1975 feeding rates increased with age, the effect being most marked for late-hatching chicks (Fig. 91). The effect was still apparent when individual watches were plotted separately (Fig. 92), which suggests that the effects of age and date of hatching were complementary in 1975. In 1976 no positive correlation between age and feeding rate was found (Fig. 93) and during a 6-h watch on 5 August and a 24-h watch on 21 August significant negative relationships were found for chicks up to 21 days old. On 5 August chicks that had hatched during the previous 5 days were fed twice as rapidly as older chicks. In 1977 no significant correlations were found between age of chicks and feeding rates, although there was a slight overall decline of feeding rates in relation to age, due to the negative correlation between feeding rate and date (App. 23).

At both S1 and U in 1977 feeding rates during the first 24 h were lower than those during days 2 and 3, possibly because many birds did not begin to forage for their chick until it had fully hatched. Nevertheless, 59% of chicks were fed during 4-h watches conducted in the first 24 h after hatching ($N = 49$). Feeding rates did not decrease just prior to fledging. A comparison of feeding rates recorded on 21 August 1977 for chicks that fledged during the following 48 h with rates for chicks more than 16 days old that did not fledge during the same period showed that those that fledged were fed at a slightly higher rate than those that did not, though the difference was not significant (Table 64). However, in 1976 and 1977 feeding rates to very old chicks (> 23 days) were, on average, low. No significant correlation was found between observed rates of feeding and chick growth rates, although the lowest growth rates in 1977, between 18 and 19 August, coincided with the lowest rate of feeding observed on 19 August (Fig. 87).

**Figure 90**
Feeding rates of chicks at plot S1 in 1975 and 1976, and at plots S1 and U in 1977 in relation to ages of chicks. Values for 1977 are derived by multiplying rates observed over 4 h by three

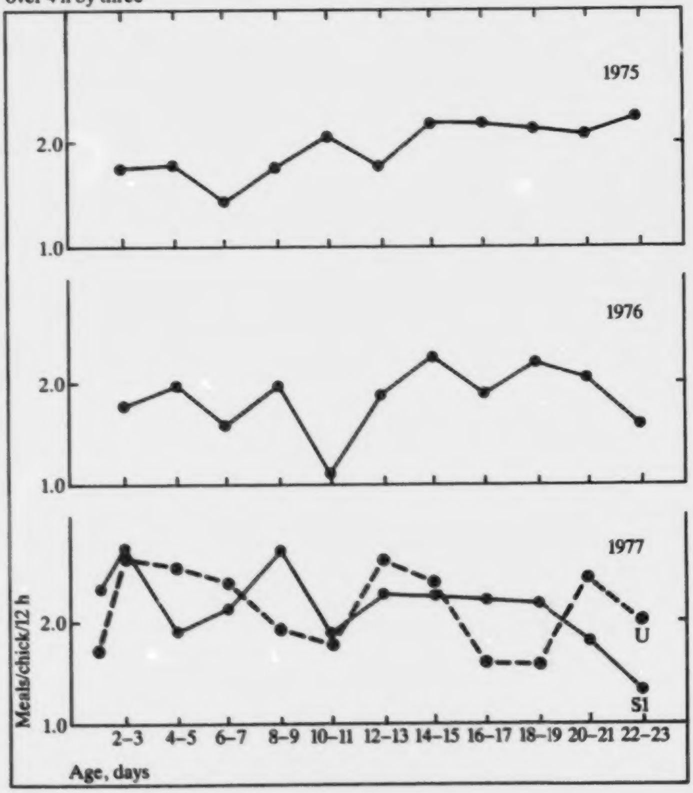


**Figure 91**
Feeding rates observed during watches at plot S1 in 1975 for three cohorts: A, hatched 25–28 July; B, 29 July – 1 August; and C, 2–5 August; D, for all age classes

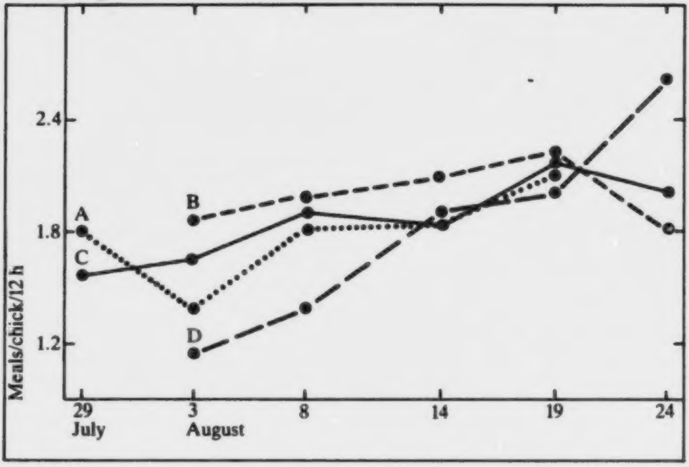


**Figure 92**
Feeding rates of chicks observed at plot S1 in 1975 in relation to the age of the chicks with four watches plotted separately: A, 8 August ($r_s = 0.86$); B, 14 August ($r_s = 0.14$); C, 19 August ($r_s = 0.44$); and D, 24 August ($r_s = 0.98$)

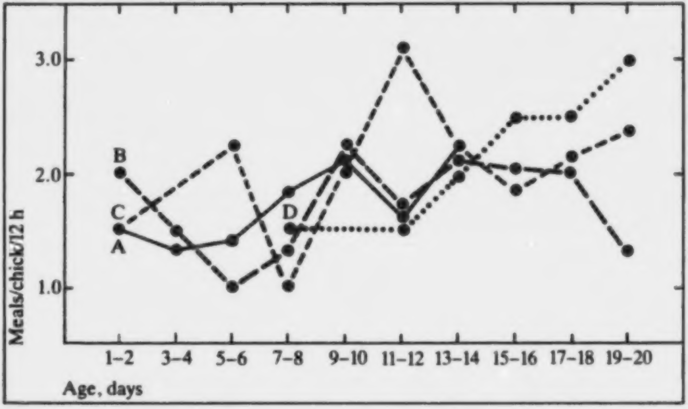
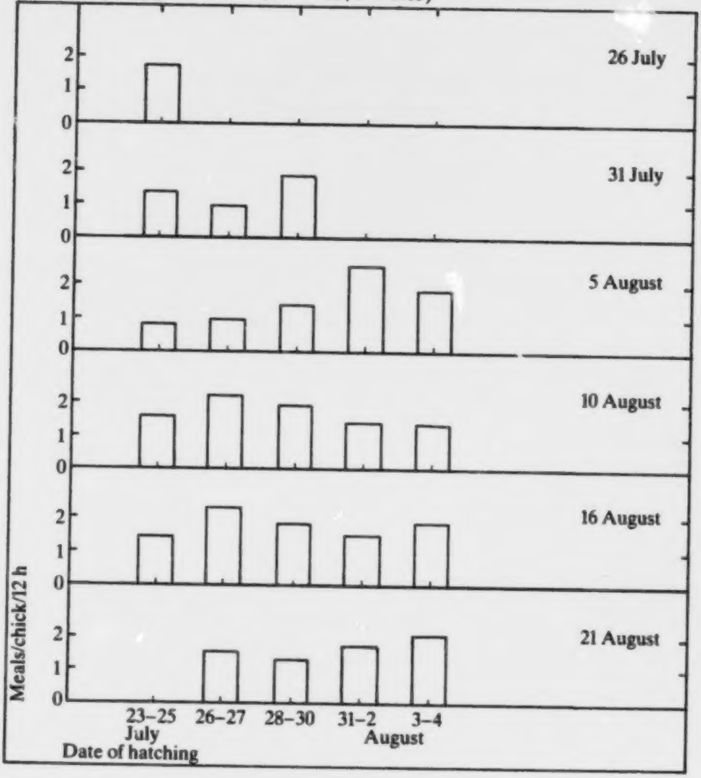


**Table 64**
Comparison of feeding rates on 21 August 1977 between chicks that fledged during the next 48 h and those over 16 days old that did not fledge until later

| Status of chick | No. of chicks | No. of meals delivered 0 | 1 | 2 | 3 | Mean no. meals |
|---|---|---|---|---|---|---|
| Chicks fledging within 48 h | 33 | 12 | 15 | 5 | 1 | 0.85 |
| Chicks not fledging | 17 | 6 | 10 | 1 | 0 | 0.71 |

**Figure 93**
Feeding rates of chicks observed during six watches at plot S1 in 1976 in relation to the date of hatching of the chicks. Rank correlation coefficients for rate of feeding with age of chicks are significant for 5 August ($r_s = -0.464$, $N = 79$, $P < 0.01$) and 21 August ($r_s = -0.282$, $N = 55$, $P < 0.05$)



## 4.3. Feeding rates and foraging ranges

Figure 94 shows time intervals between meals to individual chicks observed during 24-h watches on 31 July and 21 August 1976 and 24–25 August 1977. The distribution of intervals departs significantly from the Poisson distributions for the same means. This is probably because birds spend a large proportion of their foraging time catching food for themselves and tend to concentrate either on supplying their own needs or those of their chick. The interval between the delivery of meals after the pair had just exchanged brooding duties was not significantly different from the interval when no exchange had occurred (Fig. 94).

Observed intervals between meals can be compared with actual foraging distances in early August 1976. An aerial survey on 2 August suggested that the mean distance of feeding birds from the Prince Leopold colony was about 56 km and the maximum about

112 km. Assuming a mean flight speed of 70 km/h and a feeding rate the same as that observed 2 days earlier, the maximum time available for feeding is about 17.2 h (Table 65). Adults probably can collect food for themselves faster than they collect food for their chicks (otherwise there is no reason why they should not have the same diet as the chicks), but even if they collect their own food twice as fast as they catch fish for the chicks (in equivalent units, i.e., g/h), the time spent foraging for themselves is 83% of the total time spent on foraging. On this basis the time devoted to catching one fish for a chick on 31 July 1976 would have been 0.78 h and the time for a round trip, not including any foraging for themselves, 2.3 h. Thus, only the inter-meal

**Figure 94**
Distributions of time intervals between meals to individual chicks observed during 24-h watches at plot S1 on 31 July and 21 August 1976 and at plot U on 24–25 August 1977. Solid lines show Poisson distribution calculated for the same means. Testing the difference between the observed and Poisson distributions using the Kolmogorov–Smirnov test gives: 31 July 1976, $D = 0.205$, $P < 0.01$; and 21 August 1976, $D = 0.184$, $P < 0.01$. For 24–25 August 1977 intervals following an exchange of brooding duty (different bird) are plotted separately from those involving a bird which had recently arrived and departed again without an exchange (same bird)

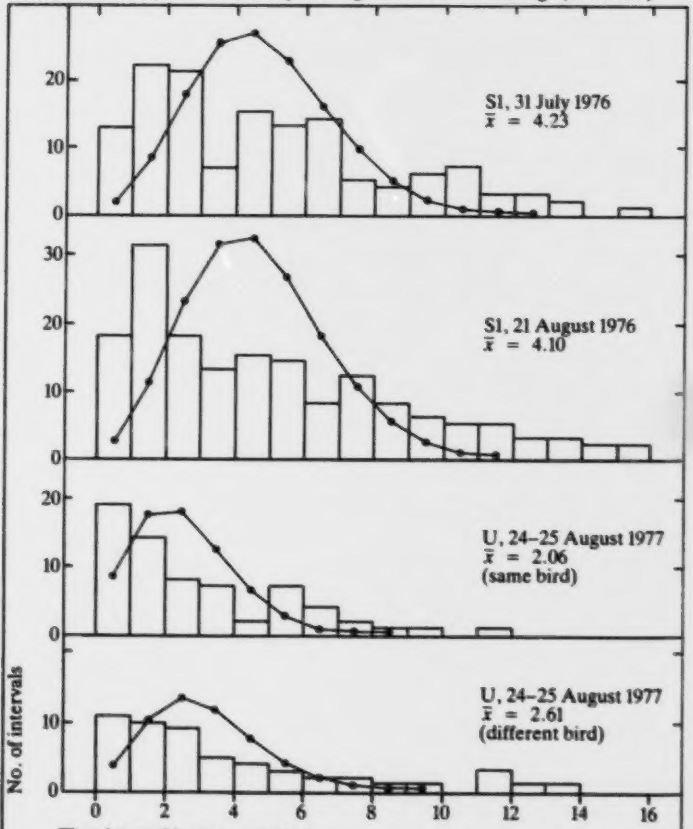


**Table 65**

**Calculation of estimates of the time spent by breeding murres foraging for themselves and for their chicks in late July and early August 1976***

Assumptions

(1) Feeding rate = 4.23 meals/chick/24 h (as on 31 July).
(2) Mean distance from colony to feeding area = 56 km (as on 2 August).
(3) Mean flight speed = 70 km/h (Portaz 1928, Vaughan 1937, Kaftanovskii 1938, Maurice 1958).
(4) Adult food requirement (wet weight of fish) = 28% of body weight/24 h (Sanford and Harris 1967).
(5) Mean adult body weight = 900 g.
(6) Mean weight of meals delivered to chicks = 12.5 g (this chapter, section 4.4).
(7) Adults can collect their own food twice as fast as they can collect food for their chicks (in wet weight/time).

| Estimates | | | |
|---|---|---|---|
| Adult food requirement: | $900 \times 0.28 \times 2$ | = | 504 g/day |
| Food delivered to chick: | $4.23 \times 12.5$ | = | 52.9 g/day |
| Travel time per feeding trip: | $\frac{56 \times 2}{70}$ | = | 1.60 h |
| Proportion of feeding time spent foraging for the chick: | $\frac{52.9}{(504) + 52.9} \times 100$ | = | 9.5% |
| Total flying time: | $1.60 \times 4.23$ | = | 6.77 h |
| Maximum time available for foraging: | $24 - 6.77$ | = | 17.23 h |
| Time spent foraging for chick: | $17.23 \times 0.095$ | = | 1.64 h |
| Total duration of a foraging trip on which the adult did not feed itself: | $1.56 + (1.64/4.23)$ | = | 1.95 h |

* Time devoted by the adults to activities other than feeding and travelling is not estimated, but this does not affect the ratio of time spent foraging for the chick to time spent foraging for themselves. Estimated foraging times therefore represent maxima.

intervals of less than 4 h could have represented foraging trips made exclusively for the chick and longer periods probably included some foraging for the adult's own food requirements. The time expended by the adults to cover their own needs suggests that changes in the rate at which food is fed to the chicks may not necessarily indicate changes in the availability of suitable fish, but changes in the availability of prey comprising the adult diet.

### 4.4. Chick diet

A total of 181 specimens of food fed to chicks was examined during the 3-year study: 28 in 1975 (6 from adults shot while flying towards the colony, 22 picked up from ledges with chicks), 16 in 1976 (all from ledges), and 137 in 1977 (5 from flying adults, 52 from chicks fitted with collars, 80 from ledges). Practically all food items were fish, mainly arctic cod *Boreogadus saida* (Table 66), which made up 82% of items in 1975, 75% in 1976, and 78% in 1977. Not all specimens of gadid fish were sufficiently preserved for the possibility of arctic cod *Arctogadus* to be ruled out (D.E. McAllister, pers. commun.), but since all positive identifications were of *Boreogadus*, all gadid specimens probably belonged to this genus.

The sample of fish obtained from chicks fitted with collars contained a higher proportion of *Boreogadus* than that picked up on the ledges in 1977 (Table 67) and this suggests that the analysis of diet based on specimens collected from the ledges may be biased. Most of the other species of fish were relatively small and, hence, particularly likely to be brought to very young chicks or pipping eggs close to hatching.

**Table 66**
Numbers of individual food items recorded in the diet of Thick-billed Murre chicks at Prince Leopold Island, 1975–77. Each item represents one meal

| Species | Year of collection | | | Totals |
|---|---|---|---|---|
| | 1975 | 1976 | 1977 | |
| *Boreogadus saida* | 23 | 12 | 104 | 139 |
| *Triglops nybelini* | 5 | 1 | 15 | 21 |
| *Triglops pingelii* | | 1 | 10 | 11 |
| *Liparis koefoedi* | | 1 | | 1 |
| *Cyclopteris jordani* | | 1 | | 1 |
| *Gammarus wilkitzki* | | | 5 | 5 |
| Totals | 28 | 16 | 134 | 178 |

**Table 67**
Proportion of fish other than *Boreogadus* delivered to chicks, according to the method of collection

| Year | Method of collection, % | | |
|---|---|---|---|
| | From ledges with eggs or chicks | From adults collected while flying towards the colony | From chicks fitted with collars |
| 1975 | 29 (17)* | 0 (6) | |
| 1976 | 25 (16) | | |
| 1977† | 27 (77) | 0 (5) | 9 (47) |
| Combined | 27 (110) | 0 (11) | 9 (47) |

* Values in parentheses are sample sizes.
† Comparing ledge and collar samples for 1977, $chi^2 = 6.38$, $P < 0.01$.

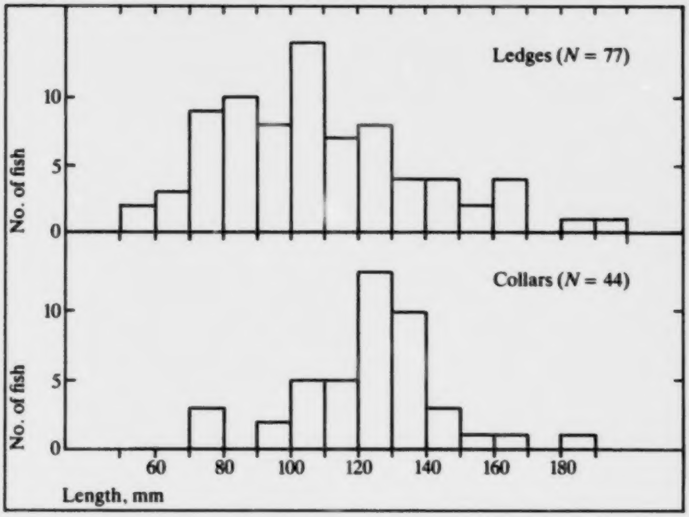
**Table 68**
Size classes of fish delivered to murre chicks, according to age of chick and method of collection

| Fish length, mm | 1977 | | | | 1976 | | |
|---|---|---|---|---|---|---|---|
| | Found on ledges beside | | | | | | |
| | Egg | ≤2-day-old chick | >2-day-old chick | Fledged chick | Adult sample collected | Collared chick sample | Collected from ledges |
| 51–60 | 2 | — | — | — | — | — | — |
| 61–70 | 1 | 1 | 1 | — | — | — | — |
| 71–80 | 2 | 7 | — | — | — | 3 | 1 |
| 81–90 | 3 | 3 | 4 | — | 1 | — | — |
| 91–100 | 2 | 3 | 3 | — | — | 2 | 2 |
| 101–110 | 4 | 6 | 3 | 1 | — | 5 | — |
| 111–120 | 1 | 4 | 1 | 1 | — | 5 | 2 |
| 121–130 | — | 4 | 3 | 1 | — | 13 | 2 |
| 131–140 | 1 | 1 | 2 | — | — | 10 | 2 |
| 141–150 | — | — | 4 | — | — | 3 | 2 |
| 151–160 | — | 1 | 1 | — | 1 | 1 | 1 |
| 161–170 | — | — | 4 | — | — | 1 | 2 |
| 171–180 | — | — | — | — | 2 | — | — |
| 181–190 | — | — | 1 | — | 1 | 1 | — |
| 191–200 | — | — | 1 | — | — | — | — |
| Totals | 16 | 30 | 28 | 3 | 5 | 44 | 14 |
| Mean* | 92.5<br>(*A*) | 101.9<br>(*B*) | 128.5<br>(*C*) | 113.0<br>(*D*) | 156.4<br>(*E*) | 125.3<br>(*F*) | 128.4<br>(*G*) |
| % not *Boreogadus* | 37.5 | 26.7 | 21.4 | 33.3 | 0 | 9.1 | 21.0 |

* Mann-Whitney $U$ test comparing sample means:

| | | |
|---|---|---|
| $A$ vs. $B$ | $z = 1.35$ | $P = 0.09$ |
| $B$ vs. $C$ | $z = 2.79$ | $P = 0.003$ |
| $A–B–C–D$ vs. $F$ | $z = 2.94$ | $P = 0.002$ |
| $A–B–C–D$ vs. $G$ | $z = 2.22$ | $P = 0.011$ |
| $C$ vs. $F$ | $z = 1.95$ | $P = 0.025$ |

**Figure 95**
Comparison of the sizes of fish picked up from ledges in 1977 with those obtained from chicks fitted with collars. Testing distributions, Mann-Whitney $U = 2317.5$, $P < 0.001$



The length of food items delivered to chicks ranged from 28 to 193 mm, the smallest being the crustacean *Gammarus wilkitzki*. The distribution of size classes varied with the method of collection; items found on the ledges were significantly smaller, on average, than those obtained from chicks with collars (Fig. 95). This, like the bias in species composition, was probably due to a preponderance in the ledge sample of fish delivered to pipping eggs or very young chicks. A comparison of fish collected on the ledges shows that those found beside eggs or chicks up to 2 days of age were significantly smaller than those found beside older chicks (Table 68). No chicks younger than 3 days old were fitted with collars.

Five fish obtained from the bills of adults shot while flying towards the colony were significantly larger than those obtained from chicks with collars, and this supports the view that shooting may select birds flying low because they are carrying relatively heavy loads. In calculating the total weight of food fed to chicks, therefore, the mean weight of fish obtained from chicks with collars is treated as representative of the typical meal size and all other samples are excluded.

For chicks fitted with collars, no significant association was found between age and the size of fish delivered. There was also no clear trend in the size of fish in relation to date, although there was some indication of a peak about 17 August and a decline in size towards the end of the month (Fig. 96). More positive evidence of a decline in the size of fish fed to the chicks in late August was obtained during observations on feeding frequency. During the early part of the season the size was recorded for only a small proportion of fish delivered during watches, because observers could not divert their

**Figure 96**
Sizes of fish collected from chicks fitted with collars in 1977 in relation to date of collection. Solid line connects mean values ( + ) for each date

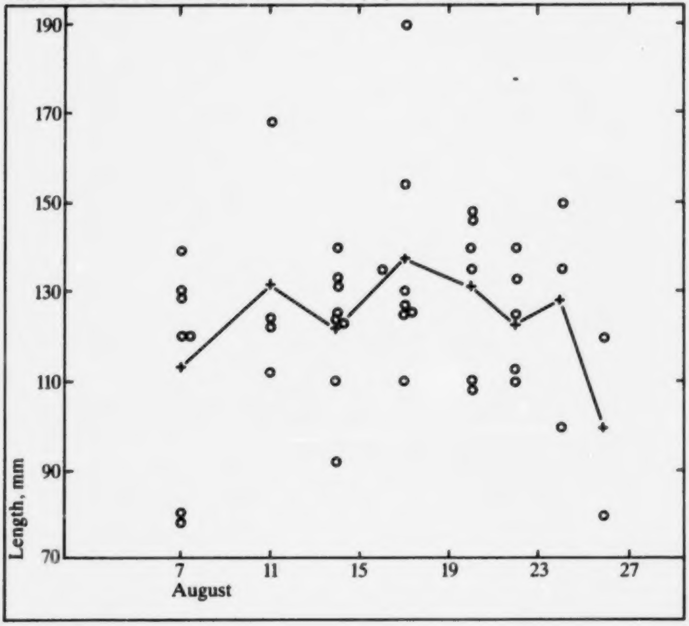


**Table 69**
Estimated sizes of fish delivered to chicks during watches in late August, 1976 and 1977*

| | Estimated size classes | | | |
|---|---|---|---|---|
| Date | <76 mm | 76–100 mm | >100 mm | *N* |
| 1977 | | | | |
| 24 August | 3 | 14 | 20 | 37 |
| 27 August | 10 | 20 | 8 | 38 |
| 30 August | 1 | 4 | 4 | 9 |
| 1976 | | | | |
| 31 August | 26 | 7 | 4 | 47 |

* Testing distributions for 1977 and lumping 27 to 30 August to increase expected frequencies, $chi^2 = 8.16$, df 2, $P < 0.02$.

**Table 70**
Estimated sizes of fish delivered to chicks on 31 August 1976, in relation to the number of times that the chicks were fed during a 12-h watch*

| No. of meals in 12 h | Estimated size classes | | | |
|---|---|---|---|---|
| | <51 mm | 51–75 mm | 76–100 mm | >100 mm |
| 1–2 | 3 | 1 | 3 | 5 |
| 3–4 | 1 | 1 | 1 | 6 |
| 5–6 | | 4 | | 2 |
| >6 | 13 | 3 | 3 | 1 |
| **Totals** | 17 | 9 | 7 | 14 |

* Rank correlation of size classes with feeding rate, $r^{s} = 0.48$, $P < 0.01$.

attention from other activities. Once most of the chicks had fledged, however, observers could estimate the size of more than 50% of the fish delivered and a comparison of watches on 24, 27, and 30 August suggests a sharp decline in the size of fish delivered to chicks (Table 69). An even higher proportion of small fish was noted on 31 August 1976, when some chicks were being fed very rapidly (nine food deliveries in 12 h) and on this date there was an inverse correlation between the rate at which chicks were fed and the estimated size of the fish delivered (Table 70), as predicted above.

### 4.5. Food consumption by chicks

The total food intake of chicks in 1977 was estimated using the following assumptions:

(1) the size of fish fed to chicks during their first 24 h is represented by items found beside pipping eggs,
(2) the size of fish fed to chicks during their second 24-h period is represented by items found beside 1- and 2-day old chicks,
(3) the size of food fed to older chicks is represented by items obtained from chicks fitted with collars,
(4) the mean rate at which fish were delivered to chicks did not alter with age and is represented by the mean rate observed between 3 and 21 August, when the majority of chicks were present, and
(5) the mean age of chicks at fledging is 20 days.

Calculations shown in Table 71 suggest that murre chicks receive an average of approximately 1100 g wet weight of fish during the chick-rearing period. The average increase in weight from hatching to fledging is 158 g, giving a conversion ratio from fish weight to chick weight of 14%. Using the same estimate for daily food intake, the conversion ratio for the period of maximum growth in weight (days 3–7) is 22%. Similar calculations for 1975 and 1976, using the same meal size but substituting the observed feeding rates for those seasons, yield conversion ratios of 25 and 24%, respectively. The fact that

**Table 71**
Calculations of total food intake by murre chicks and conversion ratio (weight increase/food ingested)

| | Calculations of total food intake | | | | |
|---|---|---|---|---|---|
| | Size of food items | | | | |
| Chick age, days | Length, mm | Weight, g* | Feeding rate, meals/day | Daily intake, g/day | Total intake |
| 1 | 92.5 | 5.6 | 4.62 | 25.9 | 25.9 |
| 2 | 101.9 | 6.6 | 4.62 | 30.1 | 30.5 |
| 3–20 | 125.3 | 12.5 | 4.62 | 57.8 | 1040.0 |
| Total | | | | | 1096.4 |

| | Calculation of conversion ratios | | | | |
|---|---|---|---|---|---|
| | | | Days 3 – 7 | | |
| Year | Feeding rate, meals/day ($A$) | Meal size, g ($B$) | Food intake ($C = A \times B \times 4$) | Wt. increase ($D$) | Conversion ratio ($D/C \times 100\%$) |
| 1975 | 3.6 | (12.5)† | 180 | 45 | 25 |
| 1976 | 3.4 | (12.5)† | 170 | 41 | 24 |
| 1977 | 4.6 | 12.5 | 232 | 51 | 22 |

* Estimated from the length using tables given in Bradstreet (1977): wet weight (mg) $= 0.0036 (\text{length, mm})^{3.12}$

† Values derived from the 1977 estimate.

conversion ratios were apparently better in the 2 years of lower feeding rates suggests that in 1977 chicks were unable to use with maximum efficiency all the food that they received during the early part of the chick-rearing period.

The levelling-off of weight increases at 220 g (19 days) in 1977 suggests that at this age and weight the energy expended for growth and maintenance was equal to the energy intake from the estimated 58 g of fish eaten per day (26% of the chick's body weight), although an increase in the caloric density of the chicks might also occur (E.H. Dunn 1975). In 1975 increase in weight levelled off at 182 g (17 days), when food intake was estimated at 23% of body weight. These figures are quite close to observations by Sanford and Harris (1967), who found that an adult murre kept at 11°C and relatively inactive required 28% of body weight in wet weight of fish per day to maintain itself. An intake of 22–25% of adult body weight in wet weight of fish is apparently normal for most fish-eating birds (Spaans 1971).

### 4.6. Discussion

The absence of any consistent relationship between the age of chicks and the rate at which they were fed suggests that, apart from the first day, adult murres feed their chicks at close to the maximum rate possible, given the constraint of maintaining their own condition.

The relationship between feeding rates, measured by the frequency with which meals are delivered, and chick growth rates is complicated by differences in the nutritional value of meals. In most cases this difference could not be measured. Where there is considerable variation in the distances travelled to feeding areas, however, birds investing a large amount of time in travelling long distances probably do so because they can find more or larger fish than birds feeding closer to the colony. The ratio of time spent travelling to time spent foraging on an average round trip on 2 August 1976 (not less than 2:1, Table 65) suggests that the observed variation in foraging distances could only be maintained if birds travelling long distances were bringing back larger fish than those feeding close to the colony. If individual birds consistently forage at a particular distance from the colony, consistent differences in feeding rates, which are not necessarily reflected in different growth rates, could result. This would explain the lack of correlation between observed feeding rates during the first five watches at S1 in 1977 and the age of chicks at fledging.

The persistent use of different feeding areas by birds from different parts of the colony provides a possible explanation for the differences in growth rates observed between chicks at plots E and S in 1977. Birkhead (1976*a*) has suggested for the Common Murre that small colonies within a few kilometres of one another may have colony-specific feeding areas. A similar explanation might also apply to the consistent differences in feeding rates between the three areas of plot S1. The existence of such intra-colony and intra-plot variation makes the interpretation of feeding rates as a measure either of food intake or foraging range rather complex. Birkhead and Nettleship (1981*a*) recorded similar effects at Coburg Island and Cape Hay in 1979.

The sharp increases in the rates of feeding observed in 1975 and 1976 after mid August were not reflected in the growth rates of late-hatched chicks, and these higher feeding rates were probably the result of birds foraging closer to the colony and bringing smaller fish to their chicks than earlier in the season. The possibility that this effect could be due to an increase in the availability of small fish is not supported by evidence from sampling in the adjacent waters of Lancaster Sound (Sekerak *et al*. 1976), which suggested that fish of the size being delivered to late chicks were actually becoming less common during August. Ward and Zahavi (1973) have suggested that large seabird colonies act as "information centres" for the transfer of information on the whereabouts of distant concentrations of food. In the case of the Prince Leopold Island colony, birds leaving the colony apparently took cues from incoming food-carrying birds concerning the initial heading to adopt (Chapter V, section 4.7). The increased feeding rates observed towards the end of the season in 1975 and 1976 coincided with the fledging of more than 50% of the chicks and hence a sharp reduction in the number of birds commuting between the colony and distant feeding grounds. The option to feed close to the colony may, therefore, have become more attractive owing to increased uncertainty concerning the whereabouts of profitable feeding areas farther away.

Further evidence of changes in feeding strategies arises from the rates of feeding observed on 5 August 1976. During the previous 3 days very marked changes in the distribution of floating ice had taken place within the foraging radius of the Prince Leopold Island colony (Nettleship and Gaston 1978), and a sharp switch in the direction from which birds were arriving at the colony occurred at the same time. Chicks hatched within the previous 5 days were fed much more rapidly than those hatched earlier, which suggests that adults that began to feed their chicks during the period of changing conditions adopted a strategy of feeding close to the colony, whereas those with older chicks persisted in trying more distant areas where they apparently had little success. Unusually heavy concentrations of floating ice continued in Lancaster Sound throughout most of August, and it may be significant that there was a reversal of the normal difference in feeding rates between areas of plot S1 during the watch on 21 August.

Because the size of meals delivered to chicks varied, there is probably little value in measuring feeding rates without some information on meal size, and this may be difficult to obtain. The most useful measure of the availability of food for the chicks is their growth rates, particularly after day 10, and the maximum weights attained. However, in assessing possible differences in food availability by this criterion, the existence of variation between different parts of the colony must also be considered. Time intervals between meals probably give little information on the distance travelled to feeding areas, because travel time is only one component of the total interval and because the amount of time spent by the adults foraging for themselves probably exceeds the amount of time devoted for foraging for their chicks.

## 5. Summary

(1) Samples of eggs taken from different parts of the colony varied in ground colour and volume and these two characters were also interrelated. Variation in ground colour probably indicates genetic heterogeneity between local sub-populations within the colony.

(2) Eggs laid in 1977 were generally smaller than those laid in 1975 and 1976, perhaps due to poor feeding conditions during the prelaying period.

(3) Growth of the chicks' primary coverts proceeded at a fixed rate, irrespective of weight increases and provided a useful criterion for ageing chicks.

(4) The weights of chicks at a given age varied significantly from year to year, being highest in 1977. Fledging weights generally ranged from 160 to 260 g.

(5) The mean growth curve for chicks weighed in 1975 reached an asymptote at 16 days, but this was not true in the other 2 years.

(6) Weight of the chicks at day 14 was positively correlated with their initial weight and negatively correlated with the date of laying, suggesting that early chicks, and those from large eggs, grew fastest.

(7) The rate at which chicks were fed was generally higher in 1977 than in the other years, except in late August when rapid rates of feeding in 1975 and 1976 were probably the result of birds foraging very close to the colony.

(8) Feeding rates had no relationship to the age of the chick between 3 and 22 days.

(9) Practically all meals delivered to chicks consisted of a single fish and the mean weight, based on those collected from collars in 1977, was 12.5 g. Items delivered to very young chicks were generally smaller than those delivered later.

(10) The principle food fed to chicks was the arctic cod *Boreogadus saida*, which accounted for more than 90% of items obtained from collars. Food material picked up from ledges contained a greater variety of prey species and was more variable in size, presumably because it included a disproportionate number of very small items intended for chicks not completely hatched at the time of delivery.

(11) The estimated daily food intake of chicks between 3 and 18 days old was 58 g fresh weight. Between 3 and 7 days old, 22–25% of this fresh weight intake was reflected in weight increases by the chick.

# Chapter V Adult weight, food, and feeding areas

# 1. Introduction

The pattern of growth observed for chicks at Prince Leopold Island and elsewhere suggests that the fledging weight of chicks, which is probably important for their subsequent survival, is controlled by the ability of their parents to feed them adequately. In view of the considerable inter-year variation in fledging weights, the strain imposed by this task must vary between seasons, and in poor years the regime is presumably quite severe. The energetic cost involved can be expected to affect the condition of parent birds and this may be reflected in their weights and in the amount of energy reserves carried in the form of subcutaneous fat.

To study the position of the Thick-billed Murre in the Lancaster Sound ecosystem we analysed food material obtained from the stomachs of birds collected as they flew towards the colony. Biases caused by differential rates of digestion of different prey organisms prevented any accurate assessment of the relative importance of different taxa, but the diet of the adult birds clearly differed considerably from the food that they delivered to their chicks. The energetic requirements of the parent birds greatly exceed those of their chicks, so that most of the time that they spend away from the colony is presumably devoted to feeding themselves, with the portion expended on chicks consisting mainly of time spent travelling between the colony and the feeding grounds. Observations on foraging distances during the chick-rearing period support this idea, with birds bringing food from distances more than an hour's flying time from the colony.

To get some idea of changes in the location of major feeding areas, birds were watched departing from the colony to determine their initial headings. Variation in these directions of departure and in the distribution of birds seen on aerial surveys combined to supplement the picture provided by studies of feeding rates, emphasizing the unpredictable changes that can occur in the position of feeding areas and the rapidity with which murres must adjust to such fluctuations. The behaviour of birds leaving the vicinity of the colony for the feeding areas is consistent with the idea that the colony acts as an "information centre", with incoming birds providing an important cue for those departing on the location of the currently profitable feeding areas.

## 2. Measurements and condition

### 2.1. Methods

We collected birds in all 3 years to examine their condition and stomach contents. Collections were made as and when conditions permitted, but we attempted to sample at least 20 birds in each of the pre-laying, incubation, and chick-rearing periods for each year. Birds were obtained by shooting, either on the cliffs or as they were flying towards the colony. In 1975, however, it became apparent that the panic caused by shooting birds on the cliffs resulted in eggs becoming dislodged. Therefore in 1976 and 1977 no birds were shot near the colony after the commencement of egg laying. Practically all birds collected during incubation and chick rearing were shot while flying towards the colony over either the south or north spits.

A few birds captured for banding were later sexed on behavioural criteria (position in copulation, etc.) and their weights were included in analyses of weight in relation to sex and season.

On all birds examined we measured the length of the wing (from the carpus flattened), the tarsus, and four bill dimensions: culmen (from the base of the feathers), from nostril to tip, the "white line" along the edge of the upper mandible, and depth at the bulge in the lower mandible. The four bill measurements were taken because, according to Storer (1952), the bill shows significantly greater sexual dimorphism than other structures and we hoped to develop a combined index to identify the sex of individual birds. This did not prove possible and only the culmen measurements are given here (App. 24).

Birds that were collected were dissected and the state of the sex organs recorded. We measured the length and maximum breadth of the male testes and the diameter of the largest ovarian follicle (i.e., oöcyte) in females and noted the state of the oviduct. We classified birds subjectively according to the amount of fat they were carrying. Initially we used four categories: (1) subcutaneous fat light, (2) fat moderate, (3) fat heavy, and (4) fat heavy and with fat bodies present on mesenteries. Later, categories 3 and 4 were combined. We checked all birds handled for a brood patch and when one was present, we measured it. Brood patches which were regressing could be identified from those which were only partially developed by the encroachment of new down at the edges and this enabled us to distinguish nonbreeders from failed breeders.

### 2.2. Measurements

Mean lengths of wing, culmen, and tarsus for all specimens collected and sexed by dissection are given in Table 72. All are close to those given by Storer (1952) for collections from the Baffin Bay area, the smallest among the Thick-billed Murre populations for which he gives measurements. Greatest sexual dimorphism was found in culmen length, but only a small proportion of birds fell outside the 95% confidence limits for the opposite sex and, hence, the measurement was not of great value as a criterion for determining the sex of individual birds.

**Table 72**
Measurements of birds collected at Prince Leopold Island during 1975–77. Only birds sexed by dissection and judged to be breeding adults are included

| | Male | | | Female | | | |
|---|---|---|---|---|---|---|---|
| Lengths | $\bar{x}$ | SD | $N$ | $\bar{x}$ | SD | $N$ | Male/Female |
| Wing, mm | 215.53 | 6.04 | 85 | 214.76 | 5.36 | 50 | 1.004 |
| Culmen, mm | 35.14 | 1.74 | 86 | 33.23 | 3.88 | 49 | 1.057 |
| Tarsus, mm | 36.27 | 1.14 | 10* | 35.44 | 1.04 | 8* | 1.023 |

| | Sexes combined | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Birds collected before 21 June | | | Birds collected after 21 June | | | | |
| | $\bar{x}$ | SD | $N$ | $\bar{x}$ | SD | $N$ | $t$ | $P$ |
| Wing, mm | 217.25 | 4.76 | 47 | 214.17 | 6.02 | 88 | 4.67 | <0.001 |

* Many tarsal measurements had to be discarded because of doubts about the comparability of the techniques used.

Birds collected during the pre-laying period (before 21 June) had significantly longer wings than breeding birds (with brood patches) collected later in the season (Table 72). This presumably indicates the effect of abrasion on rocks while the birds are at their breeding sites and suggests that wing length is unlikely to be a suitable measurement for making interpopulation comparisons in this species.

## 2.3. Condition of gonads

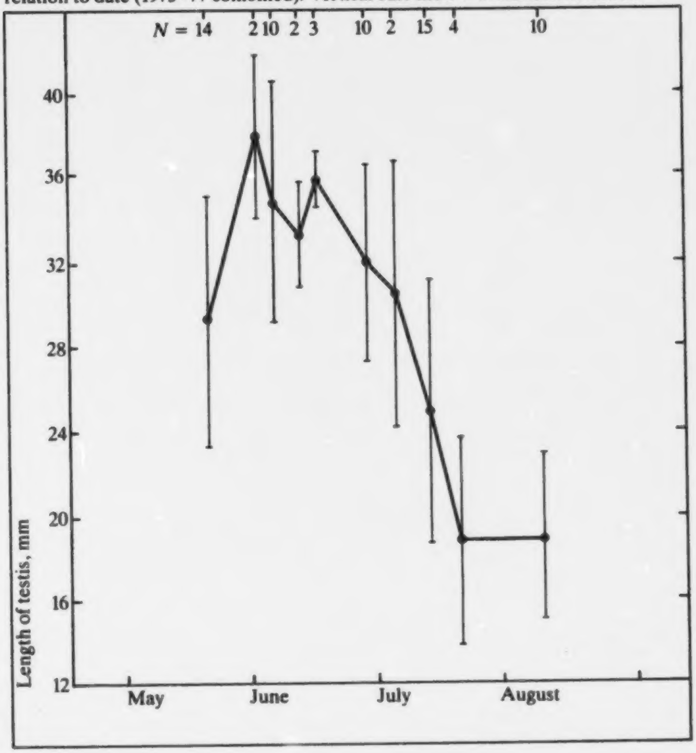
The size of testes in males collected on 23 May 1976, the earliest sample obtained, varied considerably, but by early June testes of most birds were apparently at their maximum size and dimensions remained similar throughout the month. The size decreased sharply during the first half of July, concurrent with the cessation of laying by females, and testes in most birds collected at the end of the month were completely regressed (Fig. 97). The mean maximum diameter of ovarian follicles was greatest in females collected on 30 June 1977, the middle of the laying period, falling sharply thereafter, as would be expected (Fig. 98).

## 2.4. Brood patches

Only a small proportion of birds collected prior to 15 June showed developing brood patches, but by 30 June 1977, 70% ($N = 20$) had patches fully developed (Fig. 99). On this date less than 40% of pairs had laid eggs, which suggests that the development of the brood patch is completed a few days before the egg is laid, the process apparently taking no more than 15 days. There was no indication of differences between the sexes in the development of brood patches.

Birds collected in August, including some that were carrying fish towards the colony, had brood patches beginning to grow over with down, indicating that regression of the brood patch, at least in some individuals, begins before the chicks fledge. Birds with partially developed or no brood patches examined after 15 July presumably did not breed. No indication of the proportion of non-breeders in the population can be obtained from these samples, however, because collectors intentionally selected birds carrying fish during the chick-rearing period.

**Figure 97**
Mean length of largest testis of Thick-billed Murres at Prince Leopold Island in relation to date (1975–77 combined). Vertical bars show ±1 standard deviation



## 2.5. Weight and body condition

Weights of adult birds shot or captured at Prince Leopold Island ranged from 734 to 1101 g. Mean weights varied between different stages of the breeding season and between years, but males were consistently heavier than females (mean ratio male:female 1.04) except during the incubation period in 1977. Because sample sizes were different at different times of the year, mean weights over entire seasons were not very useful, but the mean weight of all males collected was 922 g ($N = 82$) and that of females 881 g ($N = 48$). Eighty-five percent of birds weighed were between 800 and 1000 g.

For analysis, weights were divided into those obtained during the pre-laying period (before 21 June), the incubation period (21 June–21 July), and the chick-rearing period (after 21 July). Within years, males varied significantly in weight in 1976 and females in 1977 (Fig. 100). Inter-year variation was significant for males in the pre-laying period and for females in the incubation period. Weights were lower during the chick-rearing period than the pre-laying period in all

**Figure 98**
Mean diameter of largest oöcyte of Thick-billed Murres at Prince Leopold Island in relation to date (1975–77 combined). Vertical bars show ± 1 standard deviation

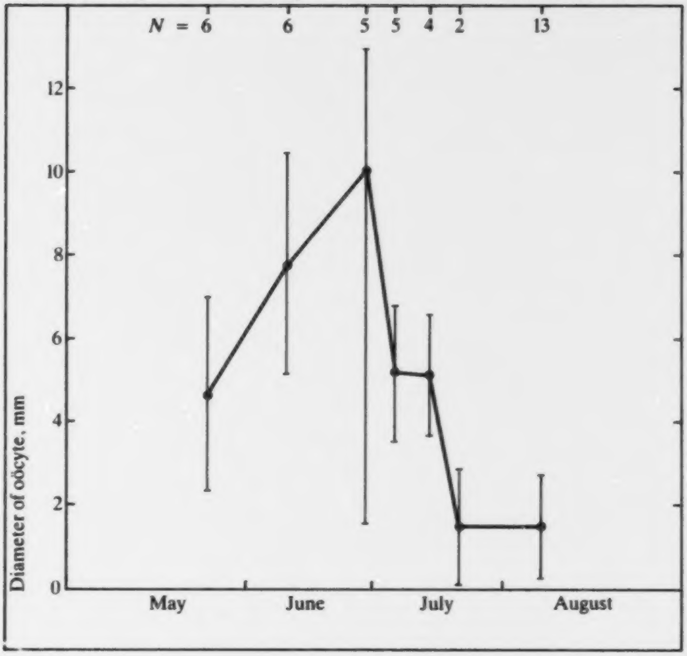


**Figure 99**
Proportion of Thick-billed Murres collected at Prince Leopold Island which had brood patches partially or fully developed or regressing, in relation to date (1975–77 combined)

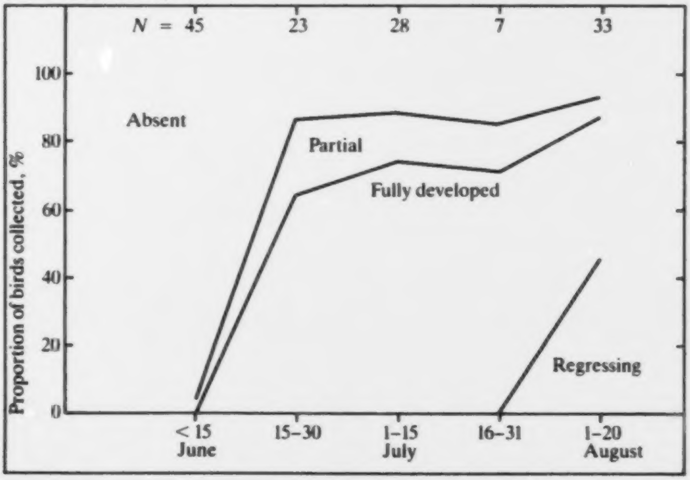
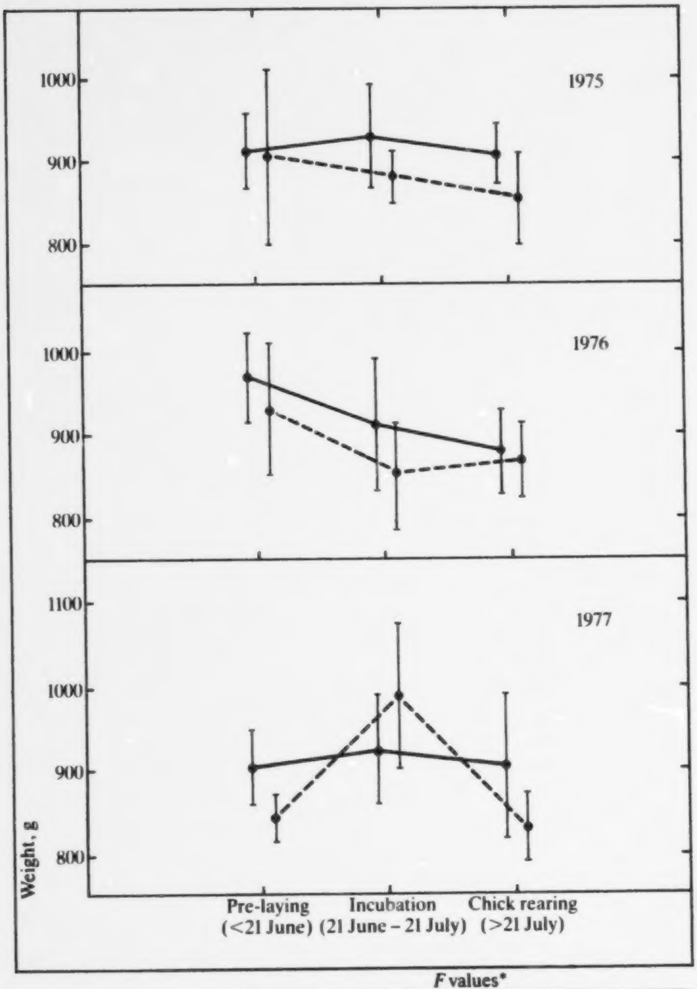


**Figure 100**
Mean weights of male (solid lines) and female (broken lines) Thick-billed Murres collected or captured at Prince Leopold Island during 1975–77, in relation to three stages of the breeding cycle. Vertical bars are ±1 standard deviation. ANOVA between and within years are given below figure



| | *F* values* | | |
|---|---|---|---|
| | Pre-laying | Incubation | Chick-rearing |
| Inter-year | | | |
| Male | 6.96(2,32)† | 0.14(2,31) | 0.62(2,19) |
| Female | 0.76(2,9) | 6.57(2,15)† | 0.85(2,21) |
| Intra-year | 1975 | 1976 | 1977 |
| Male | 2.90(2,22) | 4.44(2,33)‡ | 0.74(2,24) |
| Female | 1.09(2,16) | 0.32(2,16) | 9.31(2,11)† |

* Values in parentheses are degrees of freedom.
† $P<0.01$.
‡ $P<0.05$.

years, although the difference was very small for males in 1977. Weights of females during the incubation period in 1977 appear to have been exceptionally high.

Examination of birds for fat deposition supported the idea that differences in mean weights observed within and between years were due to changes in body condition. When data from all 3 years were combined, an overall trend towards reduction in the amount of subcutaneous fat is evident as the season progresses (Table 73). Birds collected in June 1975 and 1976 were generally fatter than those obtained in June 1977 (Table 74) and this corresponds with the lower weights observed at that period and the prediction, based on the late median date of laying in 1977, that food was relatively scarce in that year during the pre-laying period. Birds collected in May 1976 all had very heavy fat accumulation and this suggests that in that year birds arrived in the vicinity of the colony in good condition.

**Table 73**
Amounts of subcutaneous fat observed on specimens collected at three different periods. Data for 1975–77 combined*

| | Fat condition | | | |
|---|---|---|---|---|
| Period | Light | Moderate | Heavy | *N* |
| Pre-laying | 3 | 8 | 35 | 46 |
| Incubation | 14 | 18 | 13 | 45 |
| Chick-rearing | 11 | 8 | 4 | 23 |
| Totals | 28 | 34 | 52 | 114 |

* Contingency coefficient, $C = 0.521$, $chi^2 = 42.43$, df 4, $P < 0.001$.

**Table 74**
Inter-year differences in the distribution of fat classes for birds collected in June and August at Prince Leopold Island (fat condition was not recorded in August 1977)

| | Fat condition | | | |
|---|---|---|---|---|
| Year | Light-moderate | Heavy | *N* | |
| June | | | | |
| 1975 and 1976 | 2 | 11 | 13 | $Chi^2 = 7.84$, $P < 0.01$ |
| 1977 | 18 | 11 | 29 | |
| Totals | 20 | 22 | 42 | |
| August | | | | |
| 1975 | 17 | 0 | 17 | Fisher exact probability = 0.002 |
| 1976 | 2 | 4 | 6 | |
| Totals | 19 | 4 | 23 | |

**Table 75**
Mean weights of two samples of adult Thick-billed Murres collected in Lancaster Sound in August 1976. Only birds with well-developed brood patches are included

| | Male | | | Female | | |
|---|---|---|---|---|---|---|
| Location | Mean | SD | *N* | Mean | SD | *N* |
| Prince Leopold Island (10 and 12 August) | 877.62* | 52.96 | 11 | 865.57† | 44.91 | 6 |
| Eastern Lancaster Sound (12 August) | 931.40* | 59.00 | 5 | 921.75† | 41.28 | 12 |

* $t = 3.50$, $P < 0.01$.
† $t = 2.73$, $P < 0.05$.

We found significant differences in the amount of fat on birds collected in August 1976 compared with those collected in the same month in 1975 (Table 74). Because the 1976 sample was rather small, it seems unwise to place much importance on this comparison, which is not reflected by differences in weight, but it does fit the picture obtained from chick growth rates. This suggests that food was more abundant during the latter part of the chick-rearing period in 1976 than in 1975 (Chapter IV, section 3). The facts that the weights of both sexes fell sharply between the pre-laying and incubation periods in 1976 and that female weights during the latter period were lower than during chick rearing also agree with the idea that food supplies were relatively poor in July 1976.

Adult murres collected by M.S.W. Bradstreet (pers. commun.) in eastern Lancaster Sound on 12 August 1976 were significantly heavier than those collected at Prince Leopold Island in the first 2 weeks of August (Table 75). From the position of the collecting station, Bradstreet's birds must have been from the colony at Cape Hay, Bylot Island. There is no difference in measurements between these two populations (Birkhead and Nettleship 1981*a*), thus the difference probably arose partly from the weight of food carried in the proventriculus by the birds collected at sea and partly from the fact that birds obtained at the colony had used substantial food reserves during their flight from the feeding area. According to the formula given by Pennycuick (1969), a bird the size of a Thick-billed Murre should use approximately 20 g of fat in flying 100 km.

## 3. Adult diet

### 3.1. Methods

Birds were dissected as soon as possible after collection and the digestive tract examined. Food remains were preserved in 70% alcohol and identified and counted later in the laboratory. Most food recovered consisted of otoliths and fish vertebrae and fragmentary remains of crustacea, but some whole crustacea were also found. Nearly all identifiable items were in the stomach, but a few were in the proventriculus, although both otoliths and fragments of the crustacean carapace sometimes pass through the digestive tract to be eliminated in the faeces (Swennen 1977). This solid material presumably passes rapidly through the intestines.

Otoliths were paired by size to determine the number of fish represented and the most persistent portions of crustacea, usually parts of the tail, were counted. Whole specimens of crustacea and otoliths and certain fragments of crustacea were measured using a microscope and these measurements were then converted to whole body lengths using correction factors given in Bradstreet (1976).

### 3.2. Results

Only 44% ($N = 36$) of the birds collected in 1975, 56% ($N = 48$) in 1976 and 75% ($N = 48$) in 1977 had food remains in their proventriculus and/or stomach. The proportion increased as the season progressed (Table 76) and more birds collected flying towards the colony contained food than those collected from the cliffs. During the 3 years of the study we identified 15 species in the food remains: 2 fish, 12 crustacea, and 1 squid (Table 77), but only 19% ($N = 80$) of stomachs that contained food held more than one taxon.

Fish remains occurred in 96% of the stomachs that contained material. Two otoliths were identified as belonging to sculpins *Triglops* spp. and the other 237 collected were all assigned to the Gadidae, almost certainly the arctic cod *Boreogadus saida*. Crustacea occurred in 21% of stomachs that contained material, the most common genera being *Parathemisto*, *Gammarus*, and *Onisimus*, all present in 10% of stomachs. The number of crustacean taxa per stomach was positively correlated with the number of individuals of all taxa present (Fig. 101).

**Table 76**
Proportions of stomachs containing food remains among Thick-billed Murres collected in 1975–77. Birds were collected while flying towards the colony, except where specified

| | Stomachs, %* | | |
|---|---|---|---|
| Month | 1975 | 1976 | 1977 |
| May | — | 40 (20)† | — |
| June | 0 (10)† | 67 (3) | 65 (34) |
| July | 67 (9) | 70 (20) | 100 (6) |
| August | 100 (7)‡ | 100 (1)‡ | 100 (8) |

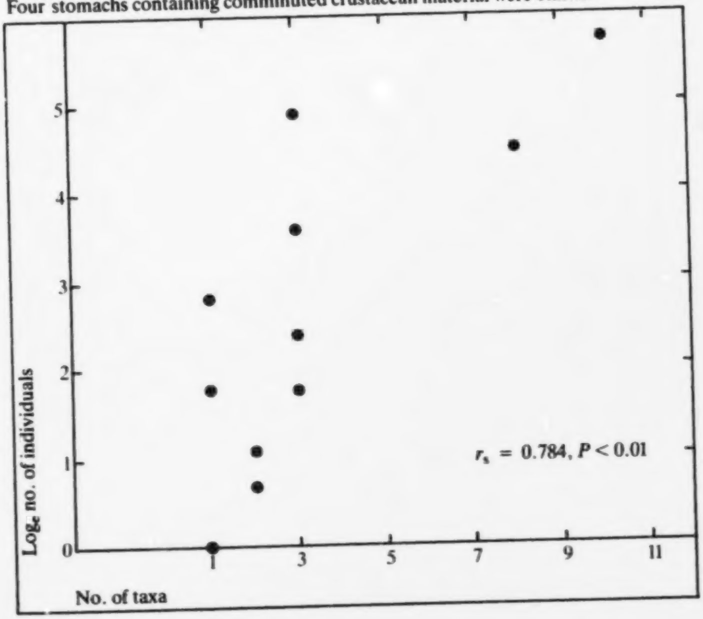
* Values given in parentheses are samples sizes.
† Birds collected on cliffs.
‡ Birds collected on cliffs excluded (1975 = 10; 1976 = 4).

**Table 77**
Frequency of different taxa in the digestive tracts of Thick-billed Murres collected at Prince Leopold Island, calculated as percentages on the number of tracts containing food remains

| | No. of tracts containing each taxon* | | | |
|---|---|---|---|---|
| Prey taxon | 1975 | 1976 | 1977 | 1975–77 |
| Fish | | | | |
| *Boreogadus saida* | 16 (100) | 26 (93) | 33 (92) | 75 (94) |
| *Triglops* spp. | — | 2 (7) | — | 2 (2) |
| Total fish material | 16 (100) | 28 (100) | 33 (92) | 77 (96) |
| Crustacea | | | | |
| *Parathemisto libellula* | — | — | 4 (11) | 4 (5) |
| *Parathemisto* (spp. unidentified) | — | 1 (4) | 7 (19) | 8 (10) |
| *Mysis oculata* | — | — | 2 (6) | 2 (2) |
| *Gammarus setosus* | — | — | 2 (6) | 2 (2) |
| *G. wilkitzkii* | — | — | 8 (22) | 8 (10) |
| *Gammarus* (spp. unidentified) | — | — | 8 (22) | 8 (10) |
| *Gamarellus homari* | — | — | 1 (3) | 1 (1) |
| *Weyprechtia pinguis* | — | — | 3 (8) | 3 (4) |
| *Onisimus littoralis* | — | — | 1 (3) | 1 (1) |
| *Onisimus* (spp. unidentified) | — | 1 (4) | 7 (19) | 8 (10) |
| *Parapleustes bicuspis* | — | — | 2 (6) | 2 (2) |
| *Pontogenia inermis* | — | — | 2 (6) | 2 (2) |
| *Apherusa glacialis* | — | — | 1 (3) | 1 (1) |
| *Anonyx sarsi* | — | — | 1 (3) | 1 (1) |
| *Monoculodes* (spp. unidentified) | — | — | 1 (3) | 1 (1) |
| Total crustacean material | 3 (19) | 3 (11) | 11 (31) | 17 (21) |
| Squid | | | | |
| *Gonatus fabricii* (?) | — | — | 1 (3) | 1 (1) |
| Total no. tracts with food items | 16 | 28 | 36 | 80 |

* Values in parentheses are percentages.

**Figure 101**
Numbers of individual crustacea recorded in relation to the number of taxa identified in the stomachs of Thick-billed Murres at Prince Leopold Island.
Four stomachs containing comminuted crustacean material were omitted



The length of prey organisms ranged from about 5 mm for the smallest crustacea up to 200 mm for the largest fish. The majority of fish were 60–180 mm in length (Fig. 102) and data from 1976 and 1977 suggested that the size of *Boreogadus* taken increased to a peak in mid July and then fell in August (Fig. 103).

A more detailed analysis of diet on the basis of birds collected at Prince Leopold Island seems inappropriate because the food remains obtained constituted a very biased sample of the food organisms ingested. This is further discussed in the following section in relation to other evidence on the feeding ecology of murres in Lancaster Sound and Barrow Strait. Full details of the numbers of organisms represented in collections from Prince Leopold Island are given in Appendices 25 and 26.

### 3.3. Interpretation of adult diets

Bradstreet (1976, 1977) analysed the contents of the digestive systems of Thick-billed Murres in Lancaster Sound and Barrow Strait in 1976. His collections were made at, or close to, areas where murres were actively feeding, but probably only those made between 7 June and 5 July and between 22 August and 1 September involved birds from Prince Leopold Island, as the other collections were within the range of birds from Cape Hay. Collections made up to 5 July were obtained at the edge of land-fast ice in Barrow Strait, while later collections were made in Lancaster Sound, some close to the shore and others in the centre of the channel.

Samples of arctic cod and of the crustacean *Parathemisto* taken from birds collected at Prince Leopold Island were larger than Bradstreet's samples obtained from birds collected on their feeding

**Figure 102**
Size distributions of *Boreogadus saida* estimated from the lengths of otoliths from the stomachs of Thick-billed Murres at Prince Leopold Island in 1976 and 1977. Inter-year difference not significant (Kolmogorov–Smirnov test)

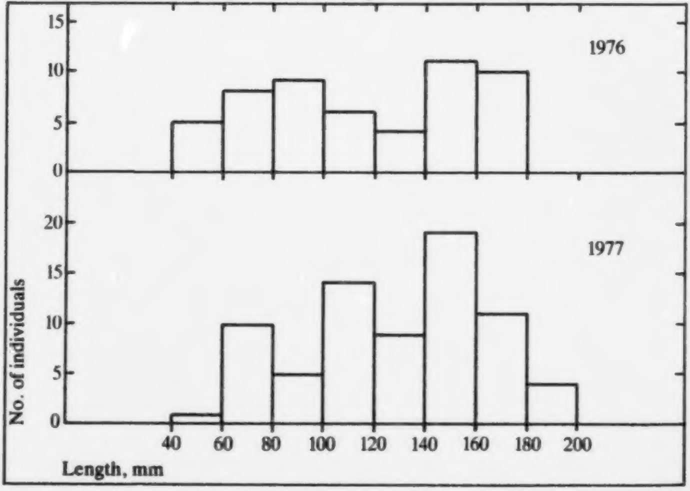
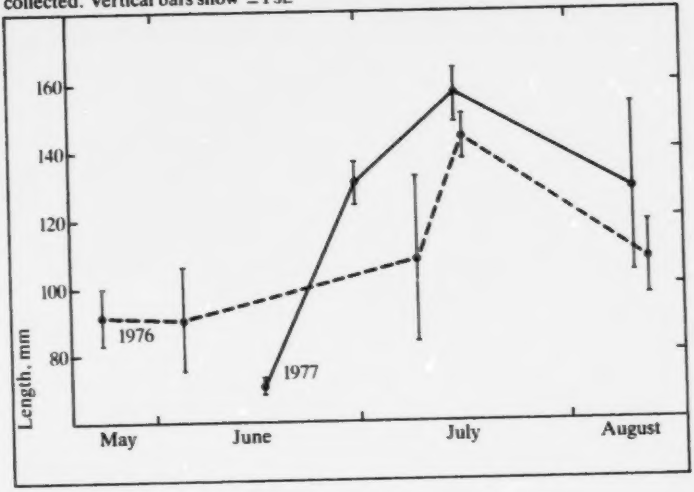


**Figure 103**
Mean lengths of *Boreogadus saida* taken from Thick-billed Murres at Prince Leopold Island in 1976 and 1977, in relation to the dates on which birds were collected. Vertical bars show ±1 SE



grounds (Figs. 104 and 105). The taxa recorded commonly by Bradstreet but not found at Prince Leopold Island (i.e., calanoid copepods and the pteropod mollusc *Limacina*) were small compared with the taxa that were identified at Prince Leopold Island. The large crustacean *Gammarus wilkitzkii*, on the other hand, occurred comparatively more frequently in the Prince Leopold Island sample than in Bradstreet's collections.

By converting each prey item identified to the dry weight equivalent of the whole organism, Bradstreet estimated the relative importance of different taxa in the diet of the Thick-billed Murre. He also discussed the possible causes of bias in his calculations. The following discussion is based partly on his reports (Bradstreet 1976, 1977) and partly on the differences observed between his results and ours.

To exemplify the problems involved in estimating the relative importance of different food organisms in the diet of the Thick-billed Murre the case of fish otoliths will be examined. Otoliths obtained from murre stomachs were frequently broken and corroded by digestive fluids. Thus at least some of the otoliths ingested are dissolved *in situ*; others are known to be voided in the faeces (Swennen 1977, Swennen and Duiven 1977). The time elapsing between ingestion of an otolith and its disappearance, by whatever means, probably varies depending on the size of the otolith and the nature of other food items ingested simultaneously. For those that dissolve, the time taken should be directly related to the thickness of the otolith and this may account for the difference in size observed between those collected by Bradstreet from birds feeding at the ice edge in Barrow Strait and those obtained during the same period at Prince Leopold Island (Fig. 104).

**Figure 104**
Comparison of size distributions of *Boreogadus saida* from Thick-billed Murres collected at Prince Leopold Island prior to 5 July in 1976 with 688 specimens from birds collected near the edge of land-fast ice by Bradstreet (1976) during the same period. Lengths calculated in both cases are from otolith measurements. Distributions differ significantly at $P < 0.01$ (Kolmogorov–Smirnov test)

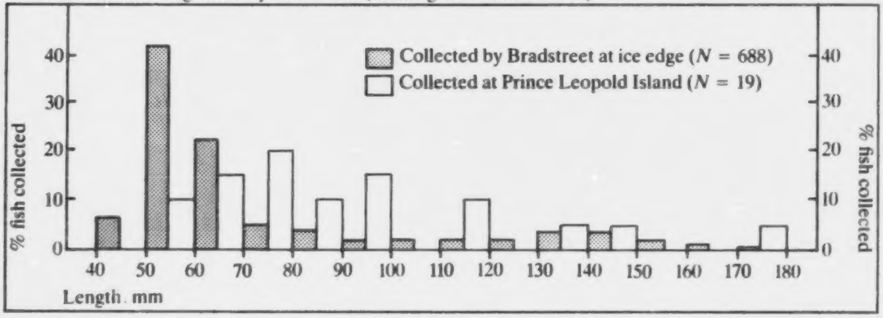
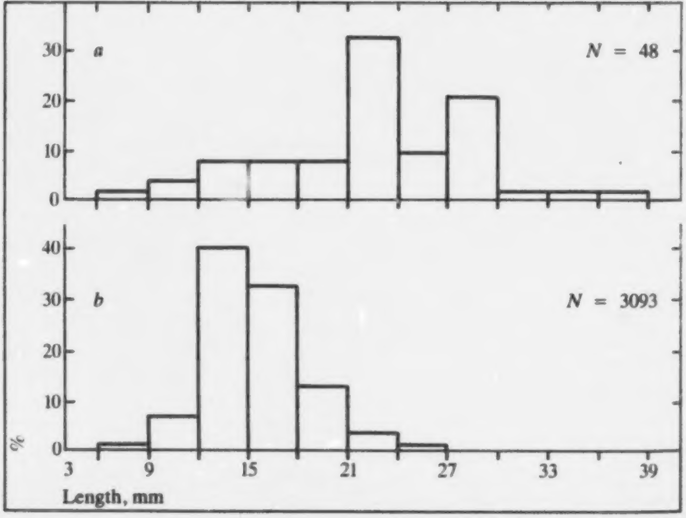


**Figure 105**
Size distributions of *Parathemisto* spp. obtained from Thick-billed Murres collected at ($a$) Prince Leopold Island between 30 June and 10 August 1977 and ($b$) on their feeding grounds in Lancaster Sound in July and August 1976 (data from Bradstreet 1976). Distributions differ significantly at $P < 0.01$ (Kolmogorov–Smirnov test)



Differential rates of disappearance caused by differences in the size of otoliths must tend to bias upwards the mean size of otoliths obtained by stomach analysis. This will be true whether birds are collected on their feeding grounds or at the colony, but in the former case the bias is likely to be smaller because the length of time elapsing between ingestion and dissection will probably be shorter.

Any aspects of size or structure that vary either within or between species and that cause differences in the rate of digestion will cause similar biases in calculations intended to reconstruct the proportional representation of prey at the time of ingestion. Differential rates of digestion may account for the difference in size detected between samples of *Parathemisto* spp. obtained from birds collected at Prince Leopold Island and those collected on their feeding grounds (Fig. 105), as well as the absence of small organisms from the former collection. Without detailed knowledge of variation in rates of digestion, any attempt to calculate the importance of different taxa in the energy budget must be treated with caution and no such attempt was made on the basis of material obtained at Prince Leopold Island.

Out of 98 Thick-billed Murres collected at the ice edge during the pre-laying period in 1976, 97% had crustacea in their digestive tracts and 93% contained fish remains (Bradstreet 1977). At Prince Leopold Island, however, no remains of crustacea were found in birds collected during the same period, although about half the stomachs examined ($N = 28$) contained the remains of fish. This suggests that crustacea were digested more rapidly than fish otoliths, an effect which would lead to the underestimation of the crustacean component in the diet in the absence of suitable correction factors. Similarly, the positive correlation observed between the number of individual crustaceans and the number of taxa present in each stomach suggests that the diversity of crustacea identified in the diet is related to the time elapsing between feeding and collection rather than to variation in the feeding preferences of different birds, although this may also occur.

The faeces of murre chicks were always white. Faeces deposited by adults, however, were predominantly white during May and June but changed to pink or red in mid July. This tint remained until the end of the season and resulted from the presence of finely comminuted chitinous material in the faeces, presumably the remains of crustacean carapaces.

The faeces colour change could occur for two reasons, both of which may be involved. Crustacea could become more important to the murre diet after mid July — a theory supported by Bradstreet's findings. Alternatively, the birds could be feeding closer to the colony or returning more rapidly to it after mid July. Thus, in June, the red-tinted crustacean remains were excreted while the birds were still away from the colony, but by July the remains were still in their digestive tracts when they landed on the cliffs. A similar explanation would apply to the observed increase in the proportion of stomachs which contained food remains during the course of the summer.

Food delivered to chicks at Prince Leopold Island was always carried in the parent's bill and we saw no regurgitations to chicks in the thousands of meal transfers that we observed, although P.G.H. Evans (pers. commun.) has occasionally observed regurgitation to chicks among Thick-billed Murres at Kipako, West Greenland. At Prince

Leopold Island, however, it seems very unlikely that any of the food found in adult stomachs during the chick-rearing period was being carried for the chicks.

An additional factor complicating the interpretation of material found in the digestive tracts of Thick-billed Murres is the possibility that some of the smaller organisms were ingested in the digestive tracts of larger ones, particularly arctic cod. Some of the whole fish obtained from chicks with collars contained virtually undigested crustacea of the same taxa identified in the stomachs of murres. We even found diatoms in the digestive tracts of the crustacea, an entire food-chain encapsulated. Where whole crustacea were found with only fragmentary remains of fish, the two were probably ingested separately; but where fragments of fish and crustacea were intermingled, the sequence of ingestion is open to question.

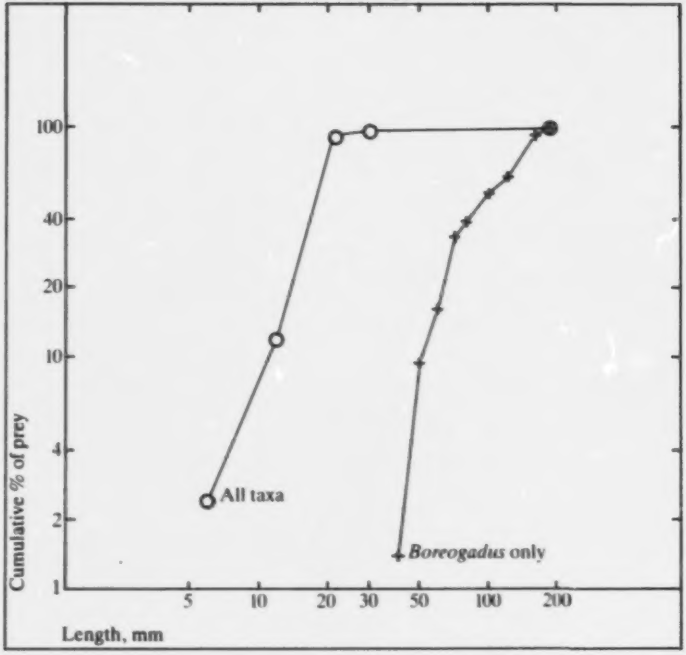
The periods spent by breeding birds on their feeding grounds were probably longer during incubation than during chick rearing (Chapter II, section 3) and this would decrease the biases created by differential rates of digestion as the season progressed. This effect may partly account for the greater apparent importance of crustacea in the diet during late July and early August compared with June and early July. However, the increase in the size of arctic cod taken between June and July, as indicated by the otoliths collected at Prince Leopold Island, runs counter to this trend and presumably indicates a real change in the size of fish captured. The same tendency is evident from Bradstreet's data, which suggest that the median length of fish taken at the Wellington Channel ice edge was 60 mm in June and early July and 120 mm in late July and August offshore in Lancaster Sound.

Gadid fish, presumably arctic cod, obtained in zooplankton tows in Lancaster Sound between 22 July and 22 August 1976 by Sekerak *et al*. (1976) were mainly between 10 and 30 mm long. Cod of these sizes were almost certainly young-of-the-year and probably hatched in May or June. The lengths estimated from otoliths collected from murres suggest that most of the arctic cod taken were 2 or 3 years of age (Andriyashev 1954).

The size distribution of prey items identified by Bradstreet from murre stomachs taken during late July and August departs very strikingly from the log-normal distribution found by Hespenheide (1971) for the sizes of prey taken by insectivorous passerines (Fig. 106). The much greater preponderance of small prey items in the case of the murres apparently reflects their very catholic feeding habits at this time of year, which suggests, in turn, that they are feeding opportunistically and that most of their prey species are found together in the same areas. This type of feeding strategy can be expected when the time involved in capturing and swallowing the prey, once it has been located, is negligible (Schoener 1971). Some of the smallest items, such as copepods, may have been ingested involuntarily in the process of taking other prey.

In view of the difficulties discussed above, what positive statements can be made concerning the diet of Thick-billed Murres at Prince Leopold Island? Bradstreet's work makes it clear that the principal prey organism throughout the breeding season is the arctic cod and our results support this. His calculations suggest that this fish constituted 90% of the dry weight food intake of birds feeding at the

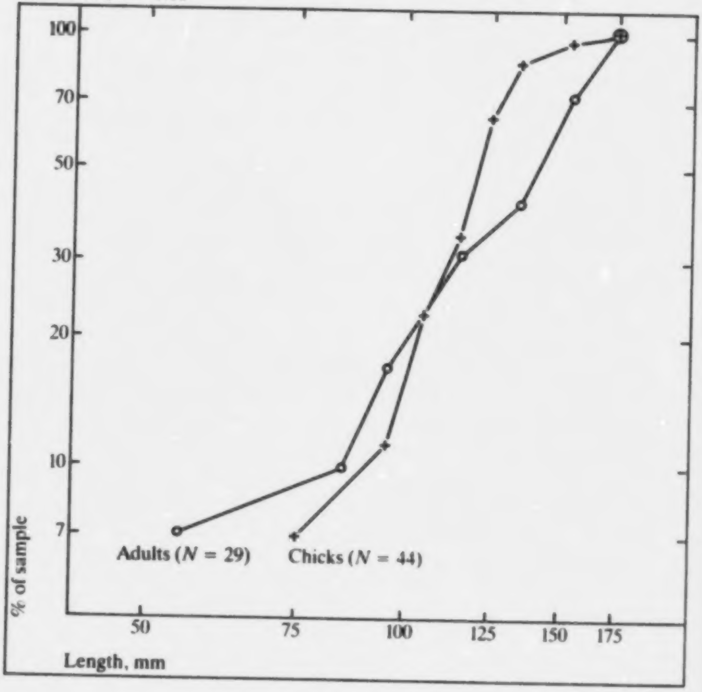
**Figure 106**
Size distribution of prey taken by adult Thick-billed Murres in Lancaster Sound (Bradstreet 1976). Both axes are plotted on a $\log_{10}$ scale



edge of fast ice in June and early July. For those feeding in open water or near shore, the proportion was 75% during 22 July–8 August and 90% during 9–26 August. The rest of the diet, in dry weight terms, consisted almost entirely of amphipod crustacea, the most common genera being *Onisimus* at the ice edge and *Parathemisto* in later collections. The importance of crustacea in the diet was almost certainly greater than estimated, for the reasons outlined above, but these estimates will probably remain the best available for the foreseeable future.

The proportion of crustacea in the adult diet during chick rearing was certainly higher than the proportion in the diet of their chicks (Chapter IV, section 4.4) and the median size of arctic cod fed to chicks was also greater than the size estimated from otoliths taken from adult stomachs during the same period (Figs. 95 and 107). Both of these observations suggest that the adults feed themselves on prey items at the smaller end of their food spectrum, selecting larger items to carry back to their chicks, a strategy that is most profitable in a situation where the time involved in travelling to and from the feeding area is a significant part of the birds' overall time-budget (Schoener 1971). Similar selectiveness by parent birds has been demonstrated for several species of terns (*Sterna* spp.) for which travelling time is also important (Dunn 1972, Lemmetyinen 1973, Taylor 1975).

**Figure 107**
Comparison of size distributions of *Boreogadus saida* from adult stomachs during chick rearing and from collared chicks in 1977. Comparing variances, $F = 3.88$, $P < 0.01$



# 4. Feeding areas

## 4.1. Methods

Information on the feeding areas used by Thick-billed Murres from the Prince Leopold Island colonies was obtained from periodic aerial surveys covering most of Barrow Strait, western Lancaster Sound, and the adjacent parts of Wellington Channel and Prince Regent Inlet. We also observed birds departing from and arriving at the colony, although only when visibility was good.

In 1975 we flew only one aerial survey, on 10 June, using a Bell 206 helicopter (Nettleship 1977*b*). In 1976 and 1977 we flew five and three surveys, respectively, in a De Havilland twin otter aircraft. The methods used on the twin otter surveys are outlined by Johnson *et al.* (1976); two observers, one on each side of the aircraft, counted all birds seen within an estimated 200 m of the flight path. The route was divided into transects and birds seen were recorded by 2-min periods. The known ground speed of the aircraft was then used to locate the position of each period so that observations could be mapped accurately. The extent of the surveys varied somewhat due to changes in the distribution of land-fast ice and poor visibility caused by fog, but the total area of water within the survey limits was approximately 24 000 km$^2$. We flew coastal surveys at 1 km from the shore and those along the edge of land-fast ice at 200 m from the ice–water interface. Full details of the methods used have been presented in Nettleship and Gaston (1978).

The density of murres observed on transects was used to calculate the total number present within the survey area, excluding the vicinity of Prince Leopold Island, which was not included in the surveys. The average density recorded on coastal transects was extrapolated to the entire area within 4 km of the coast and average densities on off-shore transects were extrapolated to the remainder of the water area. Areas covered by solid land-fast ice were excluded from the calculations, but those covered by floating ice were not. The first and last 2-min periods of off-shore transects were included with coastal transects.

Further information on distributions of birds at sea was available from aerial surveys carried out in Barrow Strait and adjacent water bodies in June and August 1974 by Davis *et al.* (1974) and in 1975 by Alliston *et al.* (1976), and along the edges of land-fast ice in 1976 by Bradstreet (1977) and Bradstreet and Finley (1977). These observations are summarized by Bradstreet (1979). Some shipboard observations were made by R.G.B. Brown during 17–19 August 1976 in Lancaster Sound and eastern Barrow Strait, including a circumnavigation of Prince Leopold Island at a distance of about 15 km (Nettleship and Gaston 1978).

## 4.2. Results of aerial surveys

### 1975

The transects carried out on 10 June covered only the area within 100 km of Prince Leopold Island. The fast-ice edge on this date stretched from Prince Leopold Island to the south coast of Devon Island, a little to the west of Maxwell Bay, but the survey did not follow the ice edge. A dense concentration of murres was observed in the centre of Prince Regent Inlet, approximately 50 km south of the colony, among loose ice pans resulting from the breakup, only a few days previously, of the land-fast ice in the inlet.

Aerial surveys by Alliston *et al.* (1976) in June revealed large concentrations of murres along the fast-ice edge north of Prince Leopold Island and also along the east coast of Somerset Island, near the mouth of Elwin Bay. During July, when the position of the fast-ice edge had receded to western Barrow Strait and the mouth of Wellington Channel, the main concentrations continued to be along the ice edges, particularly those across Wellington Channel and between Cornwallis and Griffith islands. Smaller numbers were observed along the south coast of Devon Island. The position of the ice edges at this period was similar to that in June 1974 (Davis *et al.* 1974), when the observed distributions of murres were also very similar.

No surveys were carried out by Alliston *et al.* (1976) in late July or the first half of August, and during the second half of August relatively few murres were observed. By that time there was no fast ice within 250 km of Prince Leopold Island and those birds that were recorded showed a positive association with floating pack ice, but no particular areas of concentration were evident.

### 1976

During most of June ice edges were stable across the mouth of Wellington Channel and across western Barrow Strait from Resolute Bay, Cornwallis Island, to Limestone Island off the north-west corner of Somerset Island, via Griffith Island. These positions are similar to those observed in June 1974 and July 1975. Systematic surveys of these ice edges carried out during June and early July by LGL Ltd. revealed an average of 3000 murres, concentrated mainly in the centre of Wellington Channel. The number of birds recorded varied considerably between surveys, depending partly on the direction of the wind in relation to the position of the ice–water interface (Bradstreet and Finley 1977). Numbers at the ice edge were inversely correlated with numbers recorded during the daily counts at Prince Leopold Island (Fig. 108) and this strongly suggests that birds observed at the ice edge were part of the breeding population of the colony.

Figures 109 and 110 show the distribution of murres recorded on surveys carried out on 2 and 6 August. On the earlier survey, concentrations were observed at the edges of fast ice in Garnier Bay and along the south coast of Devon Island. Only small numbers were seen at the Wellington Channel ice edge. By 6 August the distribution of fast ice had altered considerably, due to very strong winds which cleared most of the ice out of Wellington Channel, Maxwell Bay, and Radstock Bay. Large numbers of murres were seen in the two bays, particularly along the newly-formed ice edges, and comparatively high

**Figure 108**
Numbers of Thick-billed Murres recorded at the edge of fast ice (between 1000 and 1800 h) across the southern end of Wellington Channel, in relation to attendance at the Prince Leopold Island colony in 1976 (Bradstreet and Finley 1977)

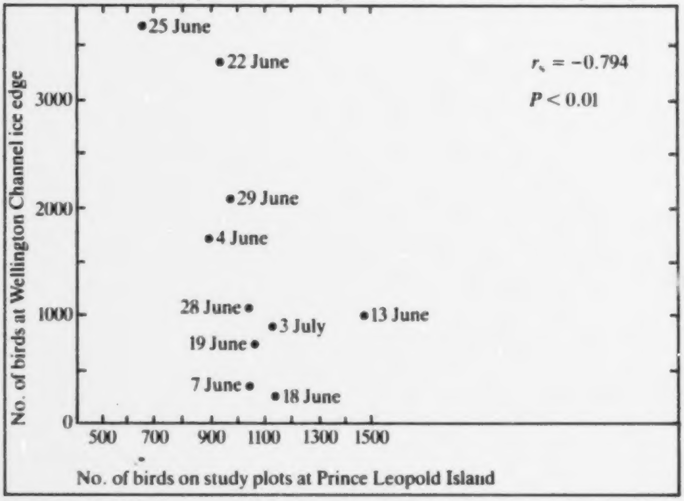
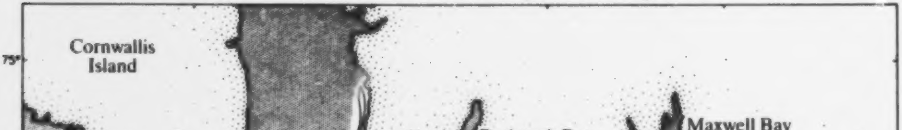


**Figure 109**
Distribution of Thick-billed Murres in the Barrow Strait survey area on 2 August 1976



Cornwallis Island
Radstock Bay
Maxwell Bay
Devon Island
Blanley Bay
Cunningham Inlet
Garnier Bay
Somerset Island
Elwin Bay
Batty Bay
Brodeur Peninsula
Birds in the air
• 1-9
○ 10-99
○ 100+
Birds on the water
• 1-9
● 10-99
● 100+
Land-fast ice
/ Flight direction of birds
0
50 km
75°
30'
74°
30'
94°
92°
90°
88°

densities were also on open water between Devon Island east of Maxwell Bay and the Brodeur Peninsula. Bradstreet (pers. commun.) observed large numbers feeding among floating pack ice north and west of Prince Leopold Island during the same period, but this area was not surveyed from the air. A comparison of the two surveys suggests that the mean foraging distance of murres from the Prince Leopold Island colonies increased between 2 and 6 August (Fig. 111), perhaps due to the break-up of the land-fast ice and the appearance of large quantities of pack ice during the intervening period.

R.G.B. Brown's observations of 17–19 August suggest that the majority of birds were feeding to the north and east of Prince Leopold Island at that time (Fig. 112). He observed birds up to 60 km from the colony carrying fish towards the island; thus, at least some of the birds foraging at this distance were breeders with chicks. During the aerial survey on 29 August, we counted only small numbers of murres, mainly scattered over open water in eastern Lancaster Sound. Surveys on 11 and 12 September revealed that very few murres remained in the area.

### 1977

Surveys were carried out on 25 June, 18 July, and 20 August. The numbers of murres recorded, their distribution between coastal and offshore waters, and estimates of the total numbers within the survey area are given in Table 78.

**Figure 110**
Distribution of Thick-billed Murres in the Barrow Strait survey area on 6 August 1976

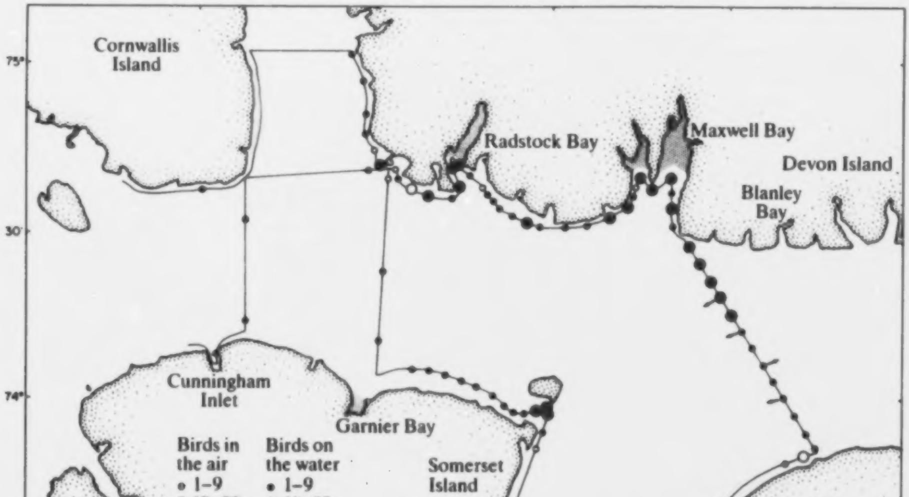

Cornwallis Island
Radstock Bay
Maxwell Bay
Devon Island
Blanley Bay
Cunningham Inlet
Garnier Bay
Somerset Island
Elwin Bay
Batty Bay
Brodeur Peninsula
Birds in the air
• 1–9
○ 10–99
○ 100+
Birds on the water
• 1–9
● 10–99
● 100+
Land-fast ice
/ Flight direction of birds
0
50 km
75°
30'
74°
30'
94°
92°
90°
88°

**Table 78**
Numbers and densities of Thick-billed Murres on coastal, off-shore, and ice-edge transects, and proportion of 2-min periods in which they were recorded on each of three surveys during 1977

| Habitat | Survey date<br>25 June | <br>18 July | <br>20 August |
|---|---|---|---|
| **Coastal** | | | |
| Total birds | — | 1884 | 296 |
| Density (birds/km²) | — | 6.20 | 2.02 |
| No. 2-min periods with murres | — | 47 (42%) | 27 (50%) |
| **Off-shore** | | | |
| Total birds | — | 199 | 56 |
| Density (birds/km²) | — | 0.93 | 0.43 |
| No. 2-min periods with murres | — | 37 (34%) | 13 (27%) |
| **Fast-ice edge** | | | |
| Total birds | 1648 | 38 | — |
| Density (birds/km²) | 17.02 | 1.40 | — |
| No. 2-min periods with murres | 37 (95%) | 7 (64%) | — |
| Ratio of densities (Coastal/offshore) | — | 6.67 | 4.70 |
| **Total** | | | |
| Coastal | — | 14 632 | 6 383 |
| Off-shore | — | 16 331 | 8 888 |
| Fast-ice edge | — | 392 | — |
| Totals | — | 31 355 | 15 271 |
| Corrected estimates* | — | 39 319 | 18 676 |

* Correction factor applied to compensate for birds missed by observer on left side of aircraft is derived from Johnson *et al.* (1976) – see text and Nettleship and Gaston (1978) for details.

**Figure 111**
Distribution of Thick-billed Murres in relation to distance from Prince Leopold Island, 2 and 6 August 1976

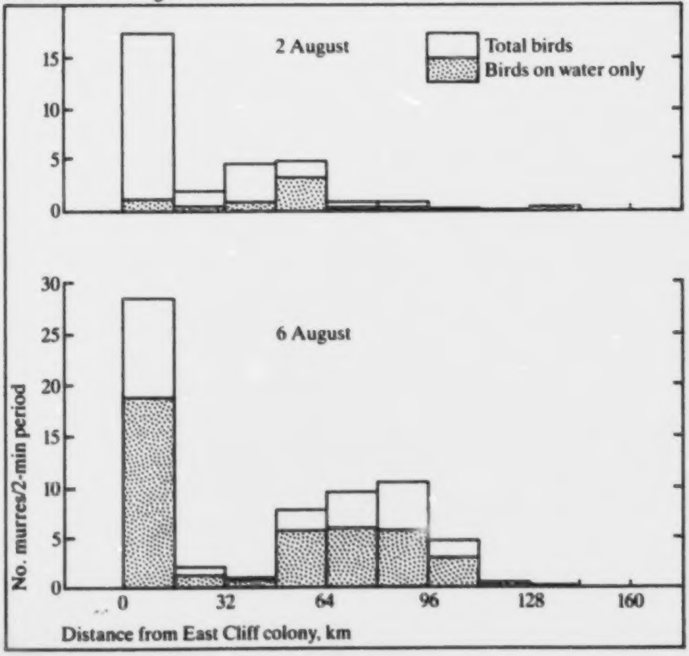
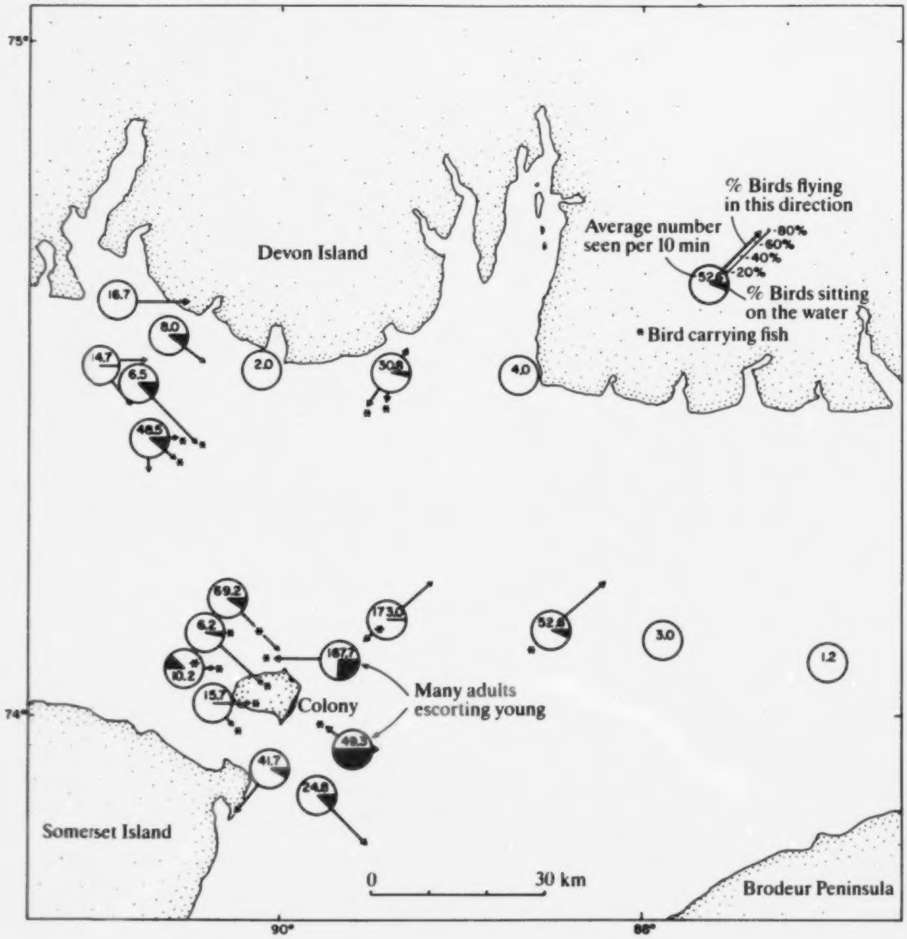


**Figure 112**
Distribution of sightings of Thick-billed Murres from CSS Hudson during 17–19 August 1976. (Data from R.G.B. Brown)


75°
74°
90°
88°
Devon Island
Somerset Island
Brodeur Peninsula
Colony
Many adults escorting young
0
30 km
% Birds flying in this direction
Average number seen per 10 min
80%
60%
40%
20%
52.6
% Birds sitting on the water
* Bird carrying fish
16.7
8.0
14.7
6.5
46.5
2.0
30.8
4.0
69.2
6.2
10.2
15.7
173.0
167.7
48.3
41.7
24.8
52.8
3.0
1.2

On 25 June we surveyed mainly the edges of land-fast ice. Large numbers of murres were at the ice edge between Prince Leopold Island and Devon Island and also south of Prince Leopold Island up to 25 km from the colony (Fig. 113). Further east along the Prince Regent Inlet ice edge numbers were lower and only a few murres were off the coast of the Brodeur Peninsula. No murres were at the ice edge across the mouth of Admiralty Inlet. Therefore, at this date most of the Prince Leopold Island population was apparently feeding within 100 km of the colony.

On 18 July we surveyed the ice edge at the mouth of Wellington Channel and part of the ice edge at the western end of Barrow Strait. No large concentrations of murres were encountered, but small numbers were seen up to 180 km from Prince Leopold Island. The only areas with high densities of murres were along the south coast of Devon Island, from Maxwell Bay eastwards, and largest numbers occurred in the inlets (Fig. 114). Moderate numbers were recorded on off-shore transects up to 60 km from the colony.

On 20 August, we saw relatively few murres, despite the fact that attendance at the colony was still high at this time. The survey extended only up to 100 km from the colony and may, therefore, have missed some important feeding areas. Most of the birds recorded were within 50 km of the colony along the north and east coasts of Somerset Island (Fig. 115). We saw an isolated concentration just off Cape York on the coast of the Brodeur Peninsula.

**Figure 113**
Distribution of Thick-billed Murres in Barrow Strait survey area on 25 June 1977

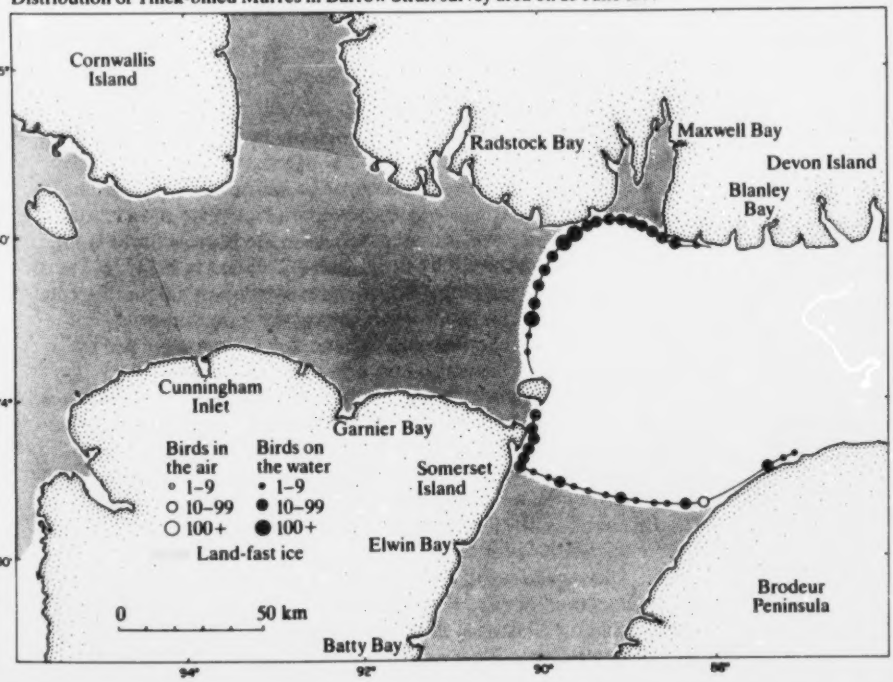
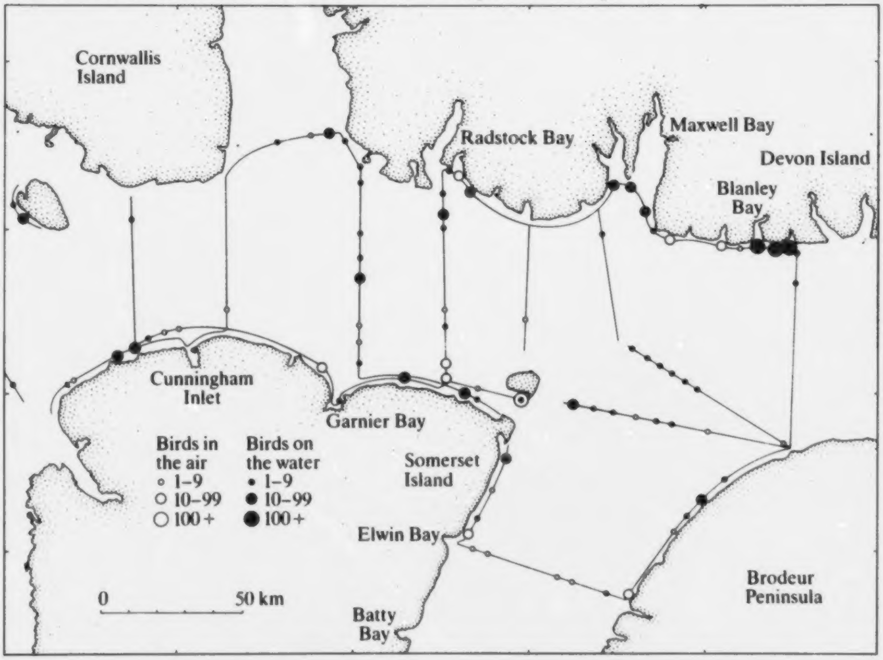

Cornwallis Island
Radstock Bay
Maxwell Bay
Devon Island
Blanley Bay
Cunningham Inlet
Garnier Bay
Somerset Island
Elwin Bay
Batty Bay
Brodeur Peninsula
Birds in the air
∘ 1–9
○ 10–99
○ 100+
Birds on the water
• 1–9
● 10–99
● 100+
Land-fast ice
0
50 km
94°
92°
90°
88°

**Figure 114**
Distribution of Thick-billed Murres in Barrow Strait survey area on 18 July 1977


Cornwallis Island
Radstock Bay
Maxwell Bay
Devon Island
Blanley Bay
Cunningham Inlet
Garnier Bay
Somerset Island
Birds in the air
○ 1–9
○ 10–99
○ 100+
Birds on the water
● 1–9
● 10–99
● 100+
Elwin Bay
Batty Bay
Brodeur Peninsula
0
50 km

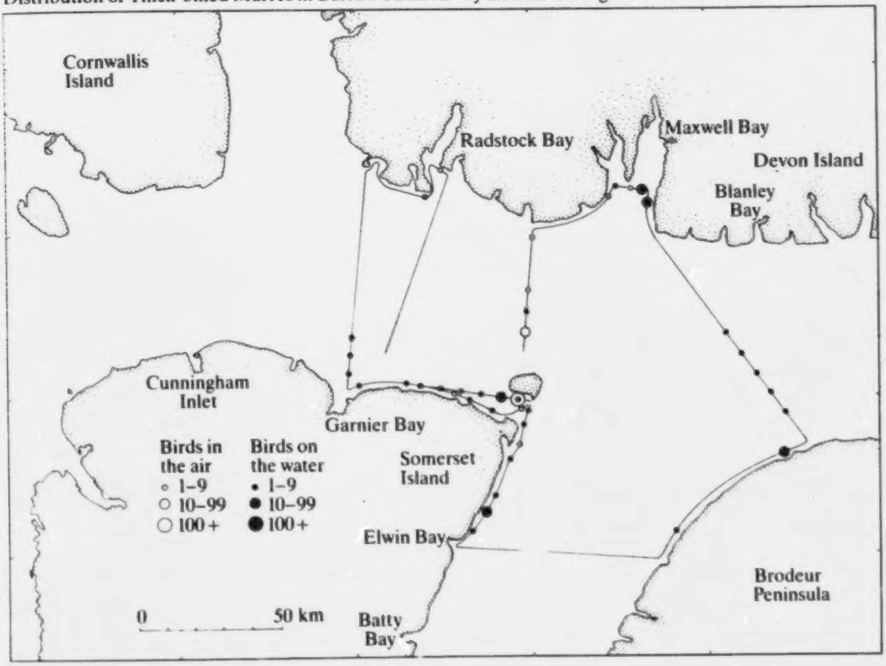
### 4.3. Habitat preference

During June and the first half of July in all years (1974–77) the distribution of Thick-billed Murres away from the vicinity of Prince Leopold Island was strongly influenced by the position of land-fast ice, with birds concentrating along the ice edge. Figure 116 shows the relative importance of different ice edges in the Barrow Strait area, during surveys carried out by Bradstreet (1979) and in 1974–76. Densities on transects flown along the ice edges were up to 100 times greater than those observed on open water during the same surveys. A similar preference for the edge of land-fast ice was recorded by Johnson *et al.* (1976) for murres in eastern Lancaster Sound.

No large concentrations of murres were recorded at the edges of land-fast ice either on 18 July 1977 or 2 August 1976, although the ice edge across the mouth of Wellington Channel was surveyed on both dates. This suggests that the attractiveness of the ice edge may be reduced as the season progresses, either because the amount of food available at the ice edge declines or because food sources become available elsewhere.

During the second half of July and throughout August higher densities of murres were recorded on coastal than on off-shore transects, except on 29 August 1976, when relatively few murres were encountered (Table 79). The surveys carried out by Alliston *et al.*

**Figure 115**
Distribution of Thick-billed Murres in Barrow Strait survey area on 20 August 1977

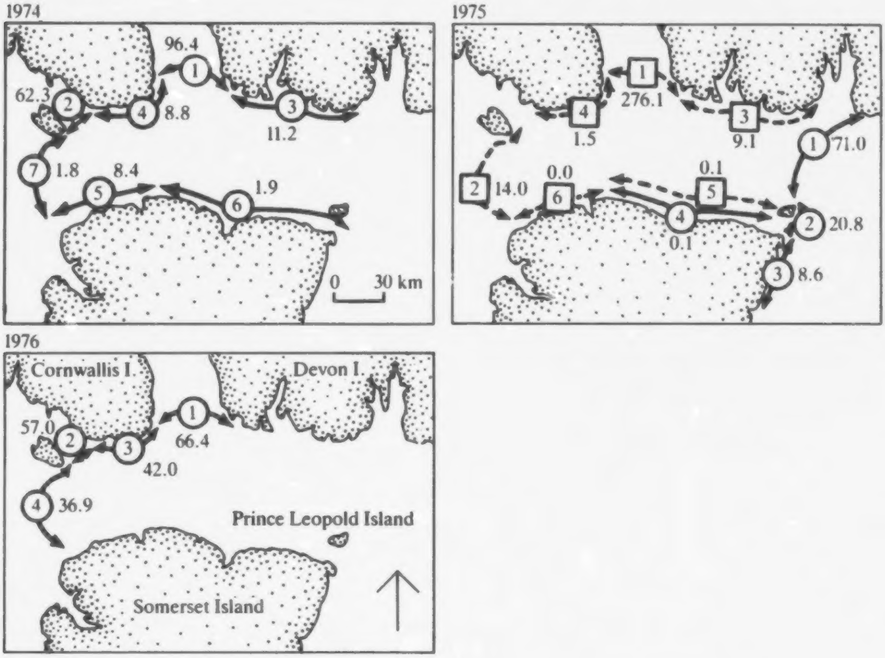

Cornwallis Island
Radstock Bay
Maxwell Bay
Devon Island
Blanley Bay
Cunningham Inlet
Garnier Bay
Somerset Island
Birds in the air
∘ 1–9
○ 10–99
○ 100+
Birds on the water
• 1–9
● 10–99
● 100+
Elwin Bay
0
50 km
Batty Bay
Brodeur Peninsula

(1976) during the second half of August 1975 revealed a different pattern; murres strongly preferred the vicinity of floating pack ice irrespective of the distance from the shore, and did not prefer coastal to off-shore waters in the absence of pack ice. A similar, and highly significant, correlation with floating pack ice, particularly where 5–25% of the water was covered, was found on the extensive series of surveys carried out in 1976 in eastern Lancaster Sound by Johnson *et al*. (1976). Boat surveys off the coast of West Greenland also suggested that Thick-billed Murres prefer the vicinity of floating ice (P.G.H. Evans, pers. commun.) but no such effect was discernible from the results of our surveys, perhaps because of insufficient sampling.

**Table 79**
Comparison of densities of Thick-billed Murres recorded on coastal and off-shore transects prior to the major fall exodus during 1976 and 1977

| | Densities (birds/km²) | | Ratio of densities |
|---|---|---|---|
| Survey date | Coastal | Off-shore | (Coastal/off-shore) |
| 2 August 1976 | 1.92 | 0.72 | 2.67 |
| 6 August 1976 | 4.26 | 1.28 | 3.33 |
| 18 July 1977 | 6.20 | 0.93 | 6.67 |
| 20 August 1977 | 2.02 | 0.43 | 4.70 |

**Figure 116**
Rank importance of various ice-edge sectors to Thick-billed Murres, 1974–76. Density indices (mean number of birds/km$^2$) are ranked for each of four periods: 1–30 June 1974; 1–20 June 1975 (—○—); 1–20 July 1975 (- - -□- - -); and 1 June – 10 July 1976. Density indices are appended to the assigned ranks (after Bradstreet 1979)



The observed association of murres with coastal waters on our surveys was due mainly to high densities encountered along the south coast of Devon Island, particularly in the fiords. The heads of these inlets are relatively shallow and receive large quantities of freshwater from streams of meltwater flowing into them from nearby glaciers and snow–ice fields. These features may attract arctic cod (Andriyashev 1954), on which the murres are more or less dependent for feeding their young, and this may account for the birds' concentration in coastal waters while rearing chicks. Large shoals of these fish have been observed in late August and September in coastal waters near Resolute Bay (E. Greene, pers. commun.) and at Creswell Bay, Somerset Island (M.S.W. Bradstreet, pers. commun.). These aggregations seem to be characteristic of pre-spawning fish (Andriyashev 1970). Most fish taken by Thick-billed Murres, however, were probably too young to be preparing to spawn and the exact circumstances under which murres catch the bulk of their food during chick rearing remain unclear. Adult murres collected offshore in August 1976 revealed a similar proportion of arctic cod in their diet to those collected in the coastal waters of Navy Board Inlet (Bradstreet 1976), which suggests that at least some arctic cod are pelagic at this time.

Murres are known to dive to depths of up to 30 m (Scott 1973), 54 m (Gurney 1913), and perhaps as deep as 70 m (Tuck and Squires 1955), but the depths of water bodies surveyed during this study are mainly greater than this and the coasts shelve steeply (Collin 1962); thus benthic fish could only be taken close inshore. The sculpins (*Triglops* spp.), fully grown individuals of which formed a regular part of the food fed to chicks, are generally regarded as bottom-living fish and these must presumably be taken in the inshore zone in relatively shallow waters.

The densities of Thick-billed Murres recorded on the water, and hence possibly feeding, ranged up to more than 100/km$^2$, but even at high densities they were usually evenly distributed over the surface. Birds seen feeding off the south coast of Prince Leopold Island were usually well spaced and birds in the tight flocks, which were frequently present just off the colony, were rarely seen feeding. In the vicinity of the island, therefore, murres were solitary feeders, as were the Black Guillemots feeding in the same area. On aerial surveys murres were sometimes seen in flocks of up to 30 birds, each bird within a few bird lengths of the next, particularly along the edges of fast ice and in the bays on the south coast of Devon Island. Some of these birds may have been resting when observed, but changes in feeding behaviour in response to changes in the species and density of prey available should be expected and social feeding may occur in Thick-billed Murres under some circumstances, as it does in some other fish-eating birds (Murphy 1936, Scott 1973, Sealy 1973*b*, Nelson 1978).

### 4.4. Estimates of total numbers of birds at sea

Prince Leopold Island is the only breeding site of the Thick-billed Murre in Barrow Strait and its associated water bodies. It is 300 km west of the nearest colony at Cape Hay, Bylot Island; thus, birds recorded west of the northern tip of the Brodeur Peninsula probably could not have originated from anywhere other than Prince Leopold Island. Birds collected at the edge of fast ice in June and July 1976 as far west as Resolute Passage were in full breeding condition (Bradstreet 1977), and in view of the numbers involved these birds must have originated from the Prince Leopold Island colonies.

Estimates of the total numbers of murres at sea within the survey area ranged from 19 000 on 20 August 1977 to 42 000 on 6 August 1976 (Table 80). If we assume the total breeding murre population of Prince Leopold Island is 86 000 pairs and one member of each pair plus 10% of their partners are present at the colony at any one time

**Table 80**
Estimates of the total numbers of Thick-billed Murres in survey area based on densities recorded within the transects

| Survey date | No. of birds* |
|---|---|
| 2 Aug. 1976 | 21 536 |
| 6 Aug. 1976 | 41 541 |
| 29 Aug. 1976 | 2 584 |
| 18 July 1977 | 39 319 |
| 20 Aug. 1977 | 18 676 |

* Details of calculations for the 1976 surveys are given in Nettleship and Gaston (1978).

(Chapter II), then the number of breeders absent from the colony can be estimated as 77 000 birds. To this number we can add a minimum of 9000 non-breeders (one-third of the non-breeding population regularly visiting the colony, the total estimated at 15% of the breeding population) (Chapter II, section 4.5). We also can subtract 5000 to allow for birds resting on the water at the foot of the breeding cliffs, an area not covered in the aerial surveys. From these calculations, at the time of the surveys about 80 000 birds should have been at sea within the survey area. The largest estimate from the surveys, however, is only about half this figure (Table 80).

Because dense concentrations of murres were mainly confined to coastal transects and because the survey pattern covered practically all coasts within 150 km of Prince Leopold Island, it seems unlikely that any major feeding locality was missed. At the same time, we saw few birds close to the limits of the survey, except along the south coast of Devon Island, and therefore the survey apparently covered the greater part of the colony's feeding area.

All observers agreed that murres, particularly those sitting on the water, were more difficult to identify than other seabirds encountered regularly in Lancaster Sound on aerial surveys (with the exception of Dovekies, non-breeding visitants). We may also have missed some birds because they dived at the approach of the aircraft and remained submerged as it passed over the area. Estimates of numbers of Thick-billed Murres present in eastern Lancaster Sound during the summer of 1976 made from similar aerial surveys also fell well short of the number calculated from the size of the breeding population at Cape Hay (Johnson *et al.* 1976), although in this case only part of the foraging area of the colony was included within the survey. These results, therefore, suggest that a considerable proportion, perhaps as much as 50%, of murres present are overlooked on this type of survey.

### 4.5. Foraging range

During June and July 1976, when a significant proportion of birds from the Prince Leopold Island colonies were feeding at the ice edges in Wellington Channel and Resolute Passage, typical foraging distances must have ranged from 110 to 175 km. For birds travelling to Resolute Passage the 350 km round trip from the island would probably have taken about 5 h. If some of those birds recorded at this ice edge in early July were members of pairs that had already laid an egg, and if they were following the normal incubation pattern of 12-h shifts, then more than 40% of their off-duty time would have been spent in travelling.

In the second half of July and August normal foraging distances are probably shorter, with most birds feeding within 100 km of the colony. The most important areas during this period are the fiords of Devon Island, 60–100 km away. Garnier Bay, another area of possible importance in July and August, is 70 km from the colony and moderate numbers were also recorded in offshore waters up to 100 km away.

Observed feeding rates to chicks do not conflict with apparent foraging distances during chick rearing. A round trip of 200 km takes about 3 h flying and, if the chick was fed twice in each 12-h off-duty period, about 50% of the off-duty time was spent in travelling to and from the feeding area. Only in 1977 did the mean rate of feeding exceed this before late August (Chapter IV, section 4.2), but in that season, with many chicks being fed three or four times in 12 h, many birds probably were feeding within 50 km of the colony. In any case, the observed distributions of murres at sea indicate that, during chick rearing, travel time formed a very significant proportion of total time spent away from the colony.

Foraging ranges observed during chick rearing are similar to those recorded elsewhere for large colonies of Thick-billed Murres. Johnson *et al*. (1976) recorded murres commonly up to 60 km from Cape Hay, although the majority were within 30 km, and Swartz (1966) found birds from the mixed Common/Thick-billed Murre colony at Cape Thomson, Alaska, feeding up to at least 60 km away. R.G.B. Brown (pers. commun.) recorded large numbers of murres feeding and carrying fish up to 80 km from the huge colonies in Digges Sound and smaller numbers up to 160 km away. Kolthoff (1903) mentions murres, presumably *lomvia*, carrying fish towards land up to 200 km from their Spitzbergen colonies. In contrast, Tuck and Squires (1955) considered that most birds from the large Thick-billed Murre colonies on Akpatok Island fed within 16 km, but such a small foraging radius appears exceptional.

### 4.6. Observations on directions of arrival and departure at the colony

In 1976 and 1977 we observed birds arriving at the East Cliff colony from the top of the cliffs overlooking the south spit. From here we could count birds arriving from south and west of the island, the latter often cutting across the base of the spit just below the observer. We could also observe birds outbound towards the west; most of these flew down the east side of the spit and rounded the tip. When low cloud made observations from the cliff top impossible we observed from the foot of the cliffs.

No regular daily fluctuations in the numbers of birds seen arriving at the colony, such as those noted by P.G.H. Evans and party (Chapter II, section 4.3), could be detected at Prince Leopold Island. Counts made at 2-h intervals throughout the day on 29 July 1976 suggested a bi-modal pattern, but other counts did not support this observation. At 0900 h on 18 July 1976 the rate of arrivals from the west was 10 birds/min, while at the same time on 19 July 156 birds/min were recorded. Likewise, the rate fell from 62 birds/min at 1800 h on 13 July 1977 to 15 birds/min at the same time the following day. Similar sharp fluctuations in the numbers of birds seen arriving from the west were noted throughout the season in both 1976 and 1977, although in both years rates of arrival were generally higher in July than in August. Such changes presumably reflect changes in the location of preferred feeding areas.

Birds leaving the area of the colony to forage generally did so after sitting on the water at the foot of the cliffs for some time. Individual birds took off separately, but gradually joined into flocks as they travelled. Those heading westwards funnelled along the south spit, flying within 2 m of the water and forming flocks of 10–50 birds by the time they rounded the tip, about 2 km from the colony. Once flocks had formed they generally remained intact until lost from view at about 5 km from the colony. Occasionally the flock split into two groups, but more often two flocks combined as one caught up with the other.

The positions at which flocks were lost from view after passing the top of the south spit were plotted for several samples watched during July 1977, using the bearings of their final position and assuming a mean flight speed of 70 km/h. The early heading of most flocks was apparently south of west (Fig. 117). From 5 July the heading apparently altered gradually as they moved away from the colony, because groups followed for a long time showed final headings further to the west than those followed for only a short period. This type of alteration might be anticipated if birds were orientating by distant topographic features or landmarks.

Variations in the initial headings of flocks between days may have been related to weather conditions. As wind speed increased, the headings of flocks rounding the spit became more westerly and less southerly (Fig. 118), perhaps because a more westerly heading allowed the birds greater shelter from the lee of the island, since the wind for all watches was coming from between the north-west and north-east.

**Figure 117**
Final positions of outbound flocks of Thick-billed Murres watched until lost from view on 5 July 1977 (o), or for 2 min beyond the tip of the south spit on 28 July 1977 (x). Both sets of observations were made between 2000 and 2200 h

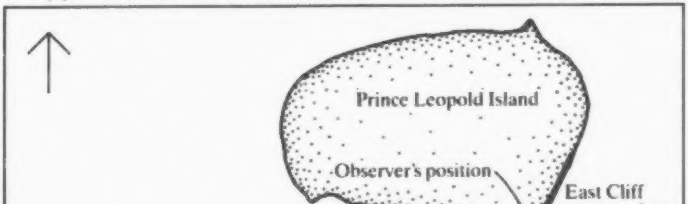

Prince Leopold Island
Observer's position
East Cliff murre colony
South Spit
Barrow Strait
Apparent route of flocks on 5 July 1977
Cape Clarence
0
5 km
Prince Regent Inlet

**Figure 118**
Mean headings of outbound flocks of Thick-billed Murres watched for at least 2 min beyond the tip of the south spit, in relation to wind speed at the time. Wind direction in all cases was between north-west and north-east

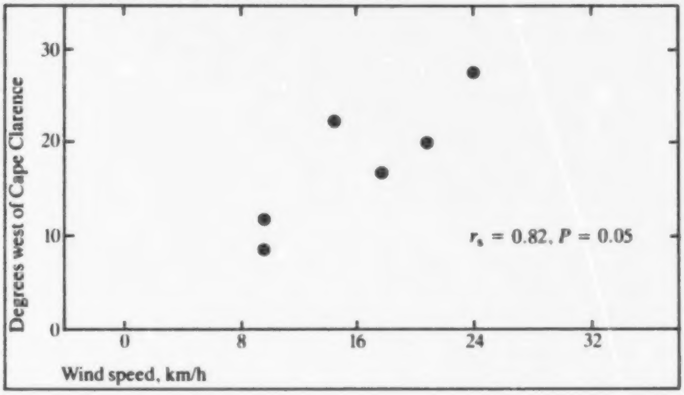


**Table 81**
Sizes of flocks and rates of departure of Thick-billed Murres recorded leaving the tip of the south spit on 6 days in 1977

| Date | Flock size (no. birds)* 1–10 | 11–20 | 21–30 | 31–40 | 41–50 | Median flock size | Rate of departure (birds/min) |
|---|---|---|---|---|---|---|---|
| 5 July | 3 | 8 | 4 | 4 | 2 | 20 | 59 |
| 12 July | 1 | 1 | 6 | 2 | 1 | 30 | 145 |
| 13 July | 2 | 6 | — | — | — | 12 | 116 |
| 16 July | 8 | 5 | 2 | 1 | 2 | 11 | 34 |
| 28 July | 8 | 2 | — | — | — | 6 | 182 |
| 7 August | 7 | 13 | 1 | 1 | — | 12 | 63 |
| Totals | 29 | 35 | 13 | 8 | 5 | | |

* Combining flock sizes of 20 and less, and those over 20, $\chi^2 = 20.2$, df 5, $P < 0.01$.

Strong northerly winds also tended to funnel incoming birds closer to the south shore of the island and under these conditions practically all incoming birds cut across the south spit.

The size of flocks departing westwards in 1977 ranged up to 50 birds, with a median of 14, and varied significantly from day to day. The variation was apparently unrelated to the total rate at which birds were departing from the colony and there was an apparent general decline in the size of outbound flocks during July (Table 81). The size of incoming flocks at the same distance from the colony was similar to that of outgoing flocks, but small flocks were hard to pick up at this range. Incoming flocks began to break up within 1–2 km of the colony as birds headed for different points on the cliffs. Birds seen carrying fish towards the colony on aerial surveys were generally solitary, and this suggests that incoming flocks formed only gradually as birds converged on the colony.

The behaviour of outbound and inbound flocks differed; inbound birds normally steered a more-or-less direct course, while outbound flocks tended to make periodic sharp course changes. Just before most of these changes of direction, the leading bird gained a few metres in altitude, followed immediately by the rest of the flock. Many outbound flocks repeated this manoeuvre once or twice a minute. After more than 50% of these manoeuvres, the flock changed direction as it lost altitude to resume flying close to the surface of the sea. A group following close behind another often responded to changes of heading by the leading group, but in these instances the group following did not rise from the surface when altering its course. In any case, the leading bird within each group normally flew slightly higher off the water than those behind and changes of leader occurred only infrequently.

Flocks may gain height before a change of flight heading for a better view and this suggests that flocks are orienting on visual cues. Visibility was excellent, however, during all observations of flock behaviour, and even from sea level birds departing round the tip of the south spit should have been able to see the high ground of the north coast of Somerset Island, at least as far west as Cape Admiral McClintock. If this was the case, then gaining height should not have been necessary.

An alternative hypothesis previously suggested by Sergeant (1951) is that the outbound flocks were orienting in response to inbound flocks, in which case, because both were flying close to the water, gaining elevation would have considerably improved their ability to detect inbound flocks. In fact, flocks travelling in both directions frequently followed the same route and avoidance action was sometimes necessary as flocks approached one another head-on. For instance, from the north coast of Prince Leopold Island on 7 July 1977 we observed birds passing in both directions in a band not more than 400 m wide at an estimated 2.5 km offshore. This route lay approximately on a line from the north spit of Prince Leopold Island to Cape Liddon, Devon Island.

Unfortunately, the headings of flocks departing from the colony gave little information on their eventual destinations. Owing to the shape of the island, birds leaving the important concentration of breeding sites around point G on the East Cliff colony would have a shorter distance to travel to reach anywhere in Barrow Strait west of Beechy Island by going south and rounding the south spit rather than going round the north end of the island. Birds seen coming or going along the south coast could therefore have been feeding at the ice edge in Wellington Channel or anywhere in Barrow Strait, except in the quadrant between the north-west and north of Prince Leopold Island. We anticipated from the south-westerly orientation of many departing flocks in 1975 that these birds were feeding somewhere near the north coast of Somerset Island, to the east of Cape Admiral McClintock (Nettleship 1977*b*). Subsequent surveys did not reveal any significant concentrations of feeding murres in this area, however, and we must assume that most birds altered their course again beyond the range of vision from the colony. The rapid changes that took place in numbers of birds coming in across or round the south spit, nevertheless, suggests that the locations of major feeding areas may change drastically in less than 24 h.

### 4.7. The location of feeding areas by foraging murres

A comparison of the distribution of murres at sea revealed by the surveys on 2 and 6 August 1976 suggests that rapid changes in the location of preferred feeding areas of the Prince Leopold Island population can take place within a few days. This is corroborated by the speed with which numbers of murres arriving at the colony from the west varied. Changes in the pattern of ice distribution in the surrounding waters may be a major cause of these abrupt switches of feeding area and a very considerable change had taken place between 2 and 6 August. The association, demonstrated by various workers (Alliston *et al*. 1976, Johnson *et al*. 1976, Bradstreet and Finley 1977, Bradstreet 1979), between the distribution of murres and floating pack ice means that the position of preferred feeding areas could alter within a single day, especially under the influence of wind and currents. Drift rates of more than 1 km/h were recorded for large pans off Prince Leopold Island, and rates of up to 40 km/day have been observed in satellite studies of ice movement in Barrow Strait (Marko 1977).

The hypothesis that outbound flocks oriented themselves by observing the flight paths of incoming flocks suggests that the breeding colony functioned as an "information centre" for the transfer of information on the position of suitable feeding areas, as suggested by Ward and Zahavi (1973). Two features of the environment in the Lancaster Sound–Barrow Strait area support this hypothesis:

(1) the position of preferred feeding areas can alter very rapidly, thus a bird that has been incubating or brooding for 12 h cannot rely on the suitability of its previous feeding areas; and

(2) visibility at sea level is frequently and unpredictably poor; thus a bird cannot rely on distant landmarks for navigation.

The effectiveness of incoming flocks as guides to outbound birds can be demonstrated by a hypothetical example. If the population of Prince Leopold Island during chick rearing divides its foraging equally among three discrete feeding areas, with approximately 30 000 pairs feeding in each, and if one area is 50 km from the colony and each pair feeds its chick four times per day, then a total of 7150 birds should be in transit between the colony and the feeding area at any one time (Table 82). Assuming incoming flocks average 20 birds, then outbound birds could expect to encounter an incoming flock on average every 280 m, which is frequent enough to keep them on course except under the worst conditions for visibility.

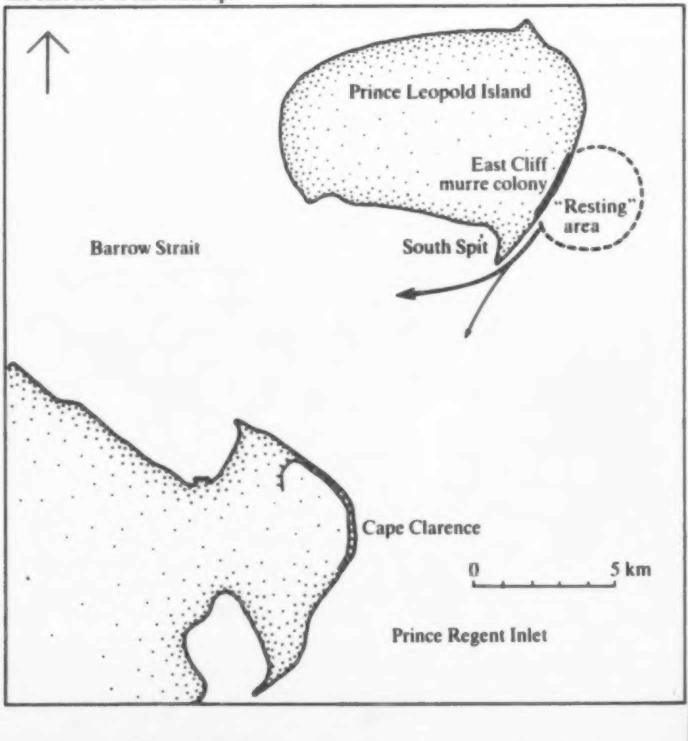
The behaviour of breeding birds observed departing from the colony fits the pattern that might be anticipated if individuals take cues from the headings of incoming or outgoing birds. Those which had just been relieved from incubation or brooding duty usually flew down to the sea, while those departing immediately after delivering a fish flew directly away from the colony (Chapter II, section 4.3). The latter birds were presumably heading back towards the feeding area that they had just left. Those which had just spent 12 h on the cliffs, however, apparently found it advantageous to join the large congregation of birds on the sea and then depart in flocks.

Owing to the shape of Prince Leopold Island, the headings of incoming birds close to the colony probably gave little clue about the area from which they originated. Birds sitting on the water at the foot of the cliffs, therefore, had to select their initial orientation. If they

**Table 82**
Hypothetical calculations of the volume and density of murre "traffic" inbound from feeding area x

| | | | | |
|---|---|---|---|---|
| Assumptions | | | | |
| Number of pairs feeding in area x | | | | 30 000 |
| Distance to area x from colony | | | | 50 km |
| Frequency of round trips per pair per day | | | | 4 |
| Realized ground speed in transit | | | | 70 km/h |
| Mean size of incoming flocks (no. birds) | | | | 20 |
| Calculations | | | | |
| Round trip time | = | $\frac{50 \times 2}{70}$ | = | 1.43 h |
| Total time spent in transit/pair/day | = | $4 \times 1.43$ | = | 5.72 h |
| No. of birds in transit at any time | = | $\frac{30\,000 \times 5.72}{24}$ | = | 7150 |
| No. of flocks inbound at any time | = | $\frac{7150}{2 \times 20}$ | = | 179 |
| Thus, average distance between flocks | = | $\frac{50}{179}$ | = | 0.28 km |

**Figure 119**
Alternative routes taken by flocks of Thick-billed Murres passing outbound down the east side of the south spit


Prince Leopold Island
East Cliff murre colony
"Resting" area
South Spit
Barrow Strait
Cape Clarence
0
5 km
Prince Regent Inlet

were uncertain about the best direction to take, they may simply have followed other, more experienced departing birds, or those which had been particularly successful on their last foraging trip. This would explain the formation of outgoing flocks.

Birds flying down the east side of the south spit were faced, on reaching the tip, with the choice of turning westwards into Barrow Strait or continuing south towards Prince Regent Inlet (Fig. 119). Out of several hundred flocks observed departing by this route the majority rounded the tip, but among the small number which headed south none were seen to break up at the point of decision. One flock which headed west altered its flight direction sharply about 1.5 km beyond the tip of the spit and flew south-east until lost from view, again without the flock splitting up. In view of the apparently scattered origins of departing flocks, following birds probably could not have known in advance which route the leading bird would take. The heading of the flock appears therefore to have been determined by the leading bird. The behaviour of flocks during regular adjustments in flight direction also points to this conclusion.

The flight directions of murres can also benefit human navigation. Tuck (1961) quotes the Norway Pilot as stating, concerning Bear Island:

> The sea around the island teems with guillemots (murres). These flocks, and the direction of their flight on approaching, together with the use of the lead, are of great value in making the island when it is foggy.

It seems inconceivable that the birds themselves should not make use of such an obvious signpost on the route between the colony and the feeding area currently favoured.

# 5. Summary

(1) Maximum development of testes and female reproductive tracts occurred from early June to early July, regressing rapidly thereafter.

(2) Brood patches began to appear by mid June and most were fully developed by the end of the month. Regression began in early August.

(3) Males were generally heavier than females and weights of both tended to decline during the season. This loss of condition was more clearly shown by a reduction in the amount of subcutaneous fat when birds collected during chick rearing were compared with those collected earlier in the season.

(4) The proportion of birds collected that contained food in their stomachs increased during the season, probably because birds fed closer to the colony during chick rearing than they had earlier.

(5) In all 3 years more than 90% of stomachs containing food yielded otoliths of arctic cod, but only 21% carried identifiable remains of any of the 14 other taxa of fish or invertebrates obtained.

(6) The predominance of the arctic cod in the diet of adult murres at Prince Leopold Island is probably exaggerated by differential digestion rates, but this fish species is certainly the most important single prey.

(7) Comparison of the size distribution of prey fed to chicks with those found in the stomachs of adults suggests that the adults feed themselves on smaller organisms and bring the large fish to the chicks.

(8) Aerial surveys showed that murres from Prince Leopold Island forage up to 200 km from the colony during pre-laying and up to 100 km during chick rearing. Distributions at sea probably change rapidly in response to changes in ice conditions.

(9) Surveys reported by Bradstreet (1979) showed that Thick-billed Murres in Lancaster Sound concentrate along the edges of land-fast ice as long as these are available within foraging range of the colony. The ice edge that often stabilizes across the southern end of Wellington Channel is particularly important for the Prince Leopold Island population. During August the fiords along the south coast of Devon Island are also very important as feeding areas for birds from Prince Leopold Island.

(10) Murres departing from the colony to feed take cues from the headings of inbound birds to determine the position of currently favourable feeding areas and the large size of the colony may be adaptive in enabling individuals to respond rapidly to changes in the distribution of feeding areas by means of the "information centre" effect.

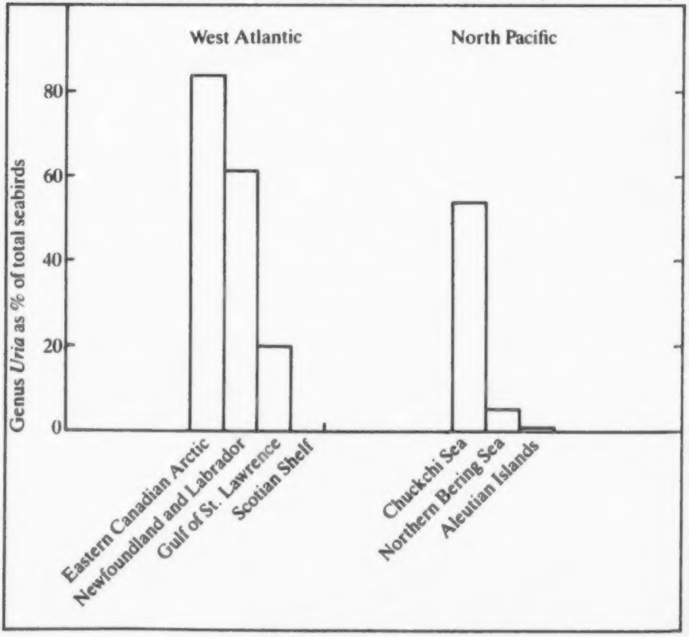
# Chapter VI Conclusions and general considerations

# 1. The Thick-billed Murre and the seabird community

The Thick-billed Murre is, by any criterion, an extremely successful species. Over much of its extensive range in arctic and subarctic waters it is, both numerically and in terms of biomass, the dominant seabird (Fig. 120), occurring in colonies that sometimes exceed one million pairs (Tuck 1961). Within its breeding range in the Lancaster Sound area the species is even more dominant, because the Atlantic Puffin and Dovekie, which nest in north-west Greenland, do not breed on the Canadian side of Baffin Bay.

In the water area defined to the west by the normal limit of permanent ice (roughly in the region of Bathurst Island), to the south by Fury and Hecla Strait, and to the east (including Lancaster Sound and adjacent waters of Baffin Bay) to about longitude 75°W, the total population of Thick-billed Murres exceeds the total population of all other seabird species (Table 83). There are, however, only four murre colonies within this area, each supporting a mean of 102 700 breeding pairs (1976–79 CWS surveys). The maximum distance between colonies is 300 km — between Prince Leopold Island and Cape Hay. Evidence for foraging ranges of up to 200 km obtained from aerial surveys indicates that, at least prior to chick rearing, the birds from

**Figure 120**
The genus *Uria* as a proportion of total numbers of seabirds, at different latitudes in the north-west Atlantic (Brown *et al.* 1975) and north-east Pacific (Sowls *et al.* 1978)



these four colonies forage over practically the entire water area under consideration (with the exception, probably, of southern parts of Prince Regent Inlet and the western end of Jones Sound).

Comparison of the seabird community in the Lancaster Sound area with other seabird communities for which suitable census data are available illustrates that Lancaster Sound is exceptional for its low diversity of species (Table 84). In the northern Pacific Ocean both species richness and equitability of the three areas decline from south to north. The same is almost certainly true of the Atlantic. Measurements of species diversity based on the Shannon–Weaver Information function (MacArthur 1965, Tramer 1969) derived from these communities cannot be compared with those for land-bird communities because the component species of seabird communities forage over widely differing areas, depending on whether they are inshore or offshore feeders. It is quite justifiable to regard seabird aggregations as communities, however, as normally all members are linked by competitive relationships, either for food or breeding-sites, or by predator–prey relationships.

**Table 83**
Census figures for seabird species breeding in the Lancaster Sound area and for Prince Leopold Island alone (numbers refer to breeding pairs from 1976–79 CWS surveys)

| | Lancaster Sound area | | Prince Leopold Island | |
|---|---|---|---|---|
| Species | *N* | % | *N* | % |
| Thick-billed Murre | 406 000 | 50.3 | 86 000 | 47.7 |
| Northern Fulmar | 275 000 | 34.1 | 62 000 | 34.4 |
| Black-legged Kittiwake | 103 000 | 12.8 | 29 000 | 16.1 |
| Black Guillemot | 17 000 | 2.1 | 4 000 | 1.7 |
| Glaucous Gull | 3 000 | 0.4 | 200 | 0.1 |
| Arctic Tern | 2 000 | 0.2 | — | |
| Thayer's Gull | 500 | < 0.1 | — | |
| Ivory Gull | 150 | < 0.1 | — | |
| Total no. of breeding pairs | 806 650 | | 181 200 | |
| Total no. of species | 8 | | 5 | |

**Table 84**
Indices of species diversity for selected seabird communities in the Atlantic and northern Pacific oceans

| Area | No. of species (*S*) | Diversity* (*H'*) | Equitability† (*J*) | Latitude (°N) |
|---|---|---|---|---|
| Lancaster Sound | 8 | 1.073 | 0.488 | 70–75 |
| Coastal Alaska:‡ | | | | |
| North of Bering Strait | 13 | 1.018 | 0.424 | 65–70 |
| North Bering Sea | 20 | 1.305 | 0.451 | 60–65 |
| Aleutian Islands | 25 | 2.030 | 0.647 | 50–55 |
| British Isles§ | 24 | 2.370 | 0.746 | 50–60 |

* $H'$ (Shannon-Weaver Information Function) = $\sum_{i=1}^{s} p_i \cdot \log_e P_i$ (Bulmer 1974)

$p_i$ = proportion of total individuals represented by species *i*.

† $J = H'/\log_e S$

‡ Figures from Sowls *et al.* (1978).
Kittlitz' and Marbled Murrelets included in the species total, but excluded from calculations of $H'$ and $J$. Common and Thick-billed Murres are treated as a single species.

§ Figures from Cramp *et al.* (1974).

A paucity of species is characteristic of plant and animal communities living under extreme physical conditions, such as those affecting desert, high montane, and polar ecosystems (Odum 1971, Colinvaux 1973). The relative poverty is exhibited at all trophic levels and results in a much simpler food web than is normally found in temperate or warmer latitudes. At the same time the shape of the species–abundance curve often becomes exaggerated, so that one, or a small number of species becomes extremely common. This observation, while placing the status of the Thick-billed Murre in the Lancaster Sound community in perspective, does nothing to explain the particular success of this bird. To do so we must examine the species' peculiar adaptations in relation to the ecosystem of which it forms a part.

The numerical dominance of the murre relative to other seabird species at the same trophic level (fulmar, kittiwake, guillemot, Arctic Tern) can be most readily understood along the lines proposed by Diamond (1978) to explain the relative abundance of seabird species nesting on tropical oceanic islands. For those species, he demonstrated that population size was positively correlated with foraging range, presumably because those birds that travel farthest have the largest food supply, in theory, at their disposal. The same is true for the species in Lancaster Sound, especially if we modify Diamond's concept to embrace not only the water area, but also the water volume available to each species (Table 85). Although both Thick-billed Murres and Northern Fulmars probably forage over a similar water area, the volume available to the murres, which dive to depths of more than 20 m, is much greater than that available to the surface-feeding fulmars. Diamond's hypothesis, however, predicts only the rank order of abundance among species and does not help to explain the increasing dominance of murres as we pass from boreal towards high arctic waters (Fig. 120).

In the southern parts of its Atlantic range the Thick-billed Murre is sympatric with other fish-eating alcids: Atlantic Puffin, Razorbill, and Common Murre. Because these potential competitors are not found in the High Arctic, where the bulk of the world population of Thick-billed Murre is concentrated, the species could then utilize a broader range of prey species and hence maintain a more generalized feeding niche than would be possible in lower latitudes. It may be significant, in this context, that in an analysis of body weight in relation to bill width/gape ratios for the Alcidae, the genus *Uria* falls

**Table 85**

Volume of water potentially available for foraging to species breeding on Prince Leopold Island during the chick-rearing period

| Species | Maximum foraging* radius, km (*A*) | Diving depth, m† (*B*) | Volume index (*A* × *B*) |
|---|---|---|---|
| Thick-billed Murre | 100 | 20 | 2000 |
| Northern Fulmar | 250 | 1 | 250 |
| Black-legged Kittiwake | 60 | 1 | 60 |
| Black Guillemot‡ | 5 | 15 | 75 |

* Based on our own observations.

† Based on Belopol'skii 1957 and our own observations.

‡ Because guillemots feed mainly on the sea bottom the calculated volume index probably exaggerates the real volume available to them for foraging.

in the centre of the scale for fish-eaters. In addition, Thick-billed Murres have broader, fleshier tongues and more palatal denticles than Common Murres, features associated with taking crustacea (Bédard 1969). Spring (1971) has argued that, compared with Common Murres, Thick-billed Murres exhibit a number of other morphological characters that enable them to switch easily from a diet of fish to one of crustacea. These observations suggest that, compared to other alcids, the Thick-billed Murre is adapted to a generalized diet and this characteristic may contribute to the numerical dominance of the species in the arctic seabird community.

The paucity of species characteristic of arctic ecosystems has been variously attributed to the immaturity of these ecosystems in terms of the time that they have been in existence, their climatic instability, and their low productivity (Dunbar 1960, 1970; Pianka 1966). Simple ecosystems have traditionally been regarded as inherently less stable than complex ones (Elton 1958, 1966), but recently this view has been challenged (May 1973, Webber 1974). In practice, if the instability of climatic or other physical factors leads to a low species diversity, then we can anticipate an apparent relationship between instability in animal populations and low species diversity.

The productivity hypothesis cannot readily be applied to latitudinal gradients in the diversity of seabird communities, because the productivity of marine ecosystems is determined mainly by the availability of mineral nutrients (Dugdale 1976, Lorensen 1976). Food resources available to arctic seabirds during the summer appear to exceed those available at lower latitudes, since the total biomass of birds per unit of marine area is as great in arctic as in most temperate waters.

Evidence that the availability of food varies unpredictably during the course of the season has already been discussed (Chapter 5, section 4.7). Our studies at Prince Leopold Island suggested that, while the sizes of the breeding populations of seabirds remained remarkably constant, conditions for reproduction differed considerably between years. In 1978 the sea ice never completely cleared from Lancaster Sound during the summer and probably no murre chicks survived to leave Lancaster Sound for their winter quarters in southwest Greenland and Newfoundland (Nettleship *et al.* 1980*b*). The important distinction between the situation in Lancaster Sound and conditions typical of more temperate climatic regimes is not necessarily that climatic fluctuations are greater, though they may be, but that their consequences are more drastic for the marine ecosystem. A deterioration which might, at lower latitudes, mean simply a poor breeding season, can precipitate disaster in an area close to the limits of viability for biological systems.

Pelagic fish-eating birds that take their prey by lengthy underwater pursuit (in the northern hemisphere, these include murres and other Alcidae; in the southern hemisphere, penguins Sphenisciformes and diving petrels *Pelecanoides*) are absent from tropical waters, whereas surface-feeding and plunge-diving birds are abundant. Diamond (1978) speculates that this may be due to the abundance of large predatory fish in the tropics. If this is true, then the situation apparently reflects the relative adaptive values of homoiothermy and poikilothermy in different climates. Birds and mammals (seals, whales) are presumably out-competed by fish in warmer waters. In polar regions the pendulum reaches the opposite extreme, with birds and mammals dominating their tropic level, the majority of fish being smaller and feeding directly on the plankton community.

As well as the relatively small number of birds species in Lancaster Sound, there are also relatively few fish species; only about 30 species have been recorded (McAllister and Hunter 1979) in Lancaster Sound compared with 86 species in West Greenland (Hildebrand 1948). Arctic cod is the most important species, both in numbers and biomass. It is the main food of Thick-billed Murres, and of kittiwake and fulmar chicks at Prince Leopold Island. Bradstreet (1976) found that, in terms of biomass, this species was the most important organism in the diets of all three species in Lancaster Sound during July and August. It also formed the bulk of the diet of murres and Black Guillemots collected at the edge of land-fast ice during the pre-laying period (Bradstreet 1977), and figures prominently in the diets of seals (McLaren 1958, Sergeant 1973) and whales (Hay and McClung 1974) in Lancaster Sound. The total annual production of these fish in Lancaster Sound and adjacent waters is roughly 400 000 metric tons (J.G. Hunter, quoted by Milne and Smiley 1978).

Examination of the stomach contents of arctic cod brought to murre chicks at Prince Leopold Island showed that the fish had been feeding on a variety of crustaceans and other zooplankton. In spring, arctic cod apparently feed on phytoplankton that live on the undersurface of sea-ice (Andriyashev 1970). The dominant position of the arctic cod at an intermediate trophic level (Fig. 121) means that the greater part of biological production in Lancaster Sound that reaches the top of the food pyramid is channelled through this one organism, giving it a pivotal role in the entire marine ecosystem.

The importance of the arctic cod in the diet of all fish-eating birds breeding on Prince Leopold Island raises the possibility that interspecific competition for food may be occurring. The results of our

**Figure 121**
The position of *Boreogadus saida* in the Lancaster Sound ecosystem

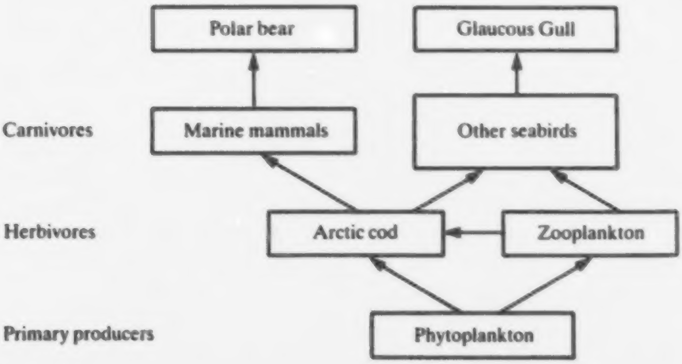


**Table 86**
Generalized comparison of food brought to seabird chicks at Prince Leopold Island during July–August (values given are percentages of total fresh weight delivered; sample sizes are numbers of meals analysed)

| Prey taxa | Northern Fulmar (*N* = 50) | Black-legged Kittiwake (*N* = 13) | Thick-billed Murre (*N* = 134) | Black Guillemot (*N* = 58) |
|---|---|---|---|---|
| Fish | | | | |
| *Boreogadus saida* | 37.4 | 93.0 | 88.2 | 3.7 |
| *Triglops* spp. | — | — | 11.3 | 3.6 |
| *Gymnelis viridis* | — | — | — | 47.7 |
| *Liparis* spp. | — | — | — | 19.6 |
| Others, unidentified* | 54.8 | — | — | — |
| Total | 92.2 | 93.0 | 99.5 | 74.6 |
| Crustacea | 7.8 | 7.0 | 0.5 | 24.9 |
| Others | — | — | — | 0.5 |

* Presumably almost all *Boreogadus saida*.

aerial surveys showed that there was a tendency for all species to associate on their feeding grounds, associations being strongest between fulmars and kittiwakes and between murres and guillemots (Nettleship and Gaston 1978).

Because murres feed to depths of more than 20 m, their potential competition with surface-feeding kittiwakes and fulmars is limited. Competition with Black Guillemots seems more logical, but analysis of food delivered to Black Guillemot chicks at Prince Leopold Island showed that most of the common taxa (*Gymnelis, Liparis, Triglops*) were benthic forms, presumably taken in shallow water (Nettleship, in prep.). During spring and early summer Black Guillemots are often found in narrow cracks and leads in fast ice (Bradstreet 1979, also this study), whereas murres are rarely seen in these situations. Guillemots, with a lower wing-loading, are apparently able to take off from situations where murres would not be able to get airborne.

At Prince Leopold Island chick diets of murres, kittiwakes, and fulmars overlap more than those of murres and Black Guillemots (Table 86). The diet of Black Guillemots at Prince Leopold Island may be influenced by the competitive environment provided by the much larger population of murres. It would be interesting to examine the diet of guillemots in areas outside the range of foraging murres, such as those breeding in the large colony near Skruis Point, on the north coast of Devon Island (Nettleship 1974).

Prince Leopold Island is unique among Canadian high arctic colonies because it supports substantial numbers of five different species of seabirds, in proportions remarkably similar to those in the Lancaster Sound region as a whole (Table 83). Most other colonies in the Canadian Arctic comprise only one or two species of seabirds. The majority of Northern Fulmars breed in single species colonies, among the largest being at Baillarge Bay, Cape Liddon, Cape Searle, Cape Vera, and Hobhouse Inlet. None of these are situated on cliffs that would be suitable for murres or kittiwakes; the majority of fulmar breeding sites are located on broad ledges or sloping screes, similar to those occupied by fulmars at Prince Leopold Island (Linton and Nettleship 1977). The association of kittiwakes with Thick-billed Murres at Cape Hay and Cape Graham Moore, Bylot Island, and Coburg

Island is not unexpected as both species require similar ledge types for breeding. However, these colony sites do not have ledges suitable for fulmars, probably because the ledges are too small and narrow. Small numbers of Black Guillemots nest in association with all the other major seabird colonies, as they do along practically the entire coast of Lancaster Sound and Barrow Strait, but in lower concentrations than at Prince Leopold Island.

The presence of suitable breeding sites for all four species on Prince Leopold Island is clearly an important factor determining the multi-species composition of the colony. It seems worthwhile to look for some positive adaptive advantage accruing through the coexistence of diverse species at this location, but there was no evidence of benefit gained either from predator defence or from interspecific feeding enhancement for any of the four major species. We conclude simply that the type of nesting sites available at Prince Leopold Island and the feeding conditions in adjacent waters combine to fulfil the requirements of all four birds.

Some factors important in determining the location of the Thick-billed Murre colony at Prince Leopold Island are suggested by an examination of the position of this and other High Arctic murre colonies. Situated at the junction of Lancaster Sound, Barrow Strait, and Prince Regent Inlet, the Prince Leopold Island colony has open water extending for at least 60 km over an arc of 270°. This position gives the birds a greater area of water over which to forage than would be the case for a colony situated midway along a straight coast, and also provides more alternative feeding areas in the event that parts of the region are covered by ice. A large open-water polynia close to the island is a regular feature during the winter and a fast-ice edge frequently remains stable between Cape Clarence and the south coast of Devon Island in May and June.

The geographical location of the Prince Leopold Island colony in relation to surrounding water bodies is strikingly similar to the position of the murre colonies at Digges Sound, the largest in the Canadian Arctic (Tuck 1961), which are situated at the north-east corner of Hudson Bay. Colonies on islands farther offshore, such as those at Akpatok Island in Ungava Bay or Coburg Island enjoy an even greater advantage in terms of the total area of water within a given radius. There was no evidence that the area of water immediately surrounding Prince Leopold Island was particularly important as a feeding area, as the dense concentrations of birds seen nearby appeared normally to be resting. At Cape Hay, however, surveys by Johnson *et al*. (1976) suggested that many birds did feed close to the colony, which may be situated adjacent to a particularly rich feeding area.

## 2. Causes and consequences of coloniality in the Thick-billed Murre

The distribution of Thick-billed Murre colonies in the High Arctic poses the question of why they are so few in number and so large in size. In West Greenland and Labrador, for instance, although large colonies of more than 10 000 pairs do occur, there are also many smaller colonies of hundreds or thousands of pairs. While it is easy to imagine that Prince Leopold Island represents the most suitable spot for a colony in Barrow Strait and western Lancaster Sound, it is hard to believe that there is not one site in the rest of that area where even a single pair of murres could breed. Appeal to a causal argument (e.g., "murres are adapted to colonial breeding") is unsatisfactory as Krebs (1978) has pointed out, because it begs the question of why the murres are colonial in the first place.

Arguments put forward to explain the adaptive significance of colonial breeding in other seabirds (Kruuk 1964, Lack 1968) do not predict any advantage in aggregations of tens of thousands, rather than hundreds of birds. Closely packed ranks of murres confer protection on broad ledges against gull predation, but such congregations are discontinuous within the boundaries of the colony. There is no reason to suppose that a group of 20 birds breeding side-by-side away from the colony would be any more vulnerable than a similar array within the colony, particularly because murres have no mobbing behaviour to deter predators. Any advantage to be gained in detecting predators from the addition of extra pairs of eyes (Powell 1974) becomes negligibly small in the context of a very large colony. Large colonies, moreover, attract their own complement of resident predators, which pose a constant threat to the murres. In addition, the concentration of a large number of conspecifics in the same place, including many non-breeding birds, must deplete food resources around the colony.

The possibility that large colonies act as "information centres", enabling birds to locate suitable feeding areas by tracking incoming birds to their origin, has already been discussed (Chapter V, section 4). According to Ward and Zahavi (1973), who first formalized the idea, the value of the information centre effect depends on the dispersion and predictability of feeding areas. The effect should be most valuable when food resources fluctuate unpredictably and the distance travelled is sufficient to impose a significant energetic cost. Both of these criteria are apparently fulfilled in the case of the colony at Prince Leopold Island.

If the information centre effect is an important factor determining the size of murre colonies, then we might expect colony size to be negatively correlated with the spatial predictability of food supplies in surrounding waters. Relevant data for making this comparison are generally lacking, but one aspect of predictability, the frequency of floating ice pans, can be analysed on the basis of existing ice maps. Comparison of colony sizes with average ice cover during chick rearing (second half of July and August) reveals that, in areas where mean ice cover at this season exceeds 10%, only colonies of more than 10 000 pairs occur (Fig. 122, Table 87).

This comparison is not simply dependent on latitude, because there are no small colonies in relatively low latitudes (60–62°N) in Hudson Strait, where ice cover is highly unpredictable; whereas they occur as far as 70°N on the west coast of Greenland, which is kept clear of ice by the warm West Greenland current. Note that the information centre hypothesis does not predict the absence of larger colonies where food is predictable. If food is abundant and suitable breeding cliffs are rare, then large colonies should develop in any case. It does predict, however, that where the location of feeding areas is subject to rapid alteration, individuals choosing to breed in small colonies will be at a disadvantage compared to those breeding in large colonies.

If we accept that the information centre effect is important to murres, particularly in the High Arctic, and that it has been a major selection pressure determining colony size, then we can extend the idea to speculate and construct predictions, which are testable in the field, on the development and functioning of the high arctic colonies. During the most severe periods of the Pleistocene glaciations probably no seabird colony existed in the eastern Canadian Arctic because ice cover would have remained unbroken throughout the year (Herman 1970, Arbib 1972). Thus, practically the entire range of the Thick-billed Murre in eastern Canada must have been colonized during the last 10 000 years.

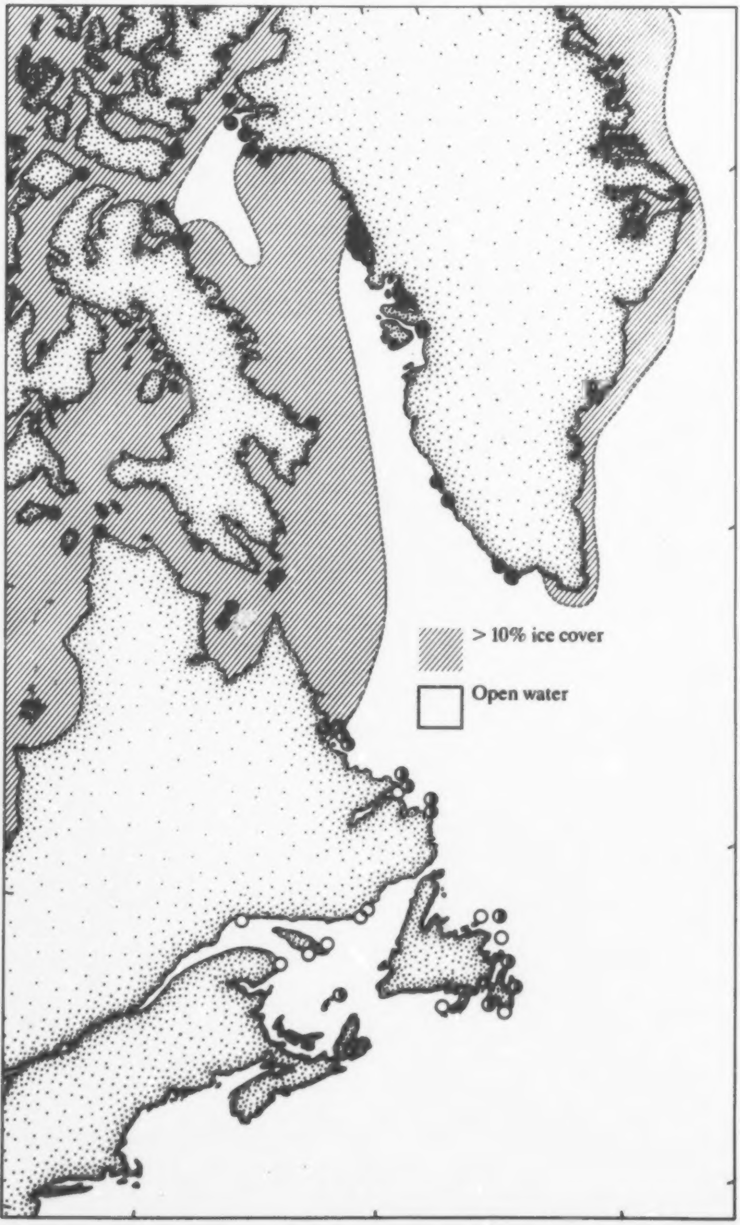
During the period of colonization, the balance of selective forces acting on the dispersive behaviours of murres must have been somewhat different from that operating today. Birds that settled away from their natal colony would have had a much greater chance of doing so successfully, because for a long time there would have been suitable but under-populated areas continually opening up to the north. During this phase, young birds probably behaved in the manner observed for boreal fulmars and Northern Gannets in Britain (Nelson 1978, Dunnet *et al.* 1979); only a small proportion settled to breed at their natal colony and the rest shifted elsewhere. Both of these species have been extending their ranges during the last 50 years

**Table 87**
Sizes of murre colonies in the western Atlantic and eastern Canadian Arctic, in relation to the frequency of drifting pack-ice during the chick-rearing period. Data on colony size are derived from Brown *et al.* (1975) and on ice cover from the Atlas of Polar Seas (U.S. Hydrographic Service 1958)*

| Zone and species | Total no. of colonies | Colony size (order of magnitude) 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|---|
| Colonies north of 60°N (*Uria lomvia*) | | | | | | | |
| Mean ice cover >0.1 | 13 | 0 | 0 | 0 | 0 | 5 | 8 |
| Mean ice cover <0.1 | 21 | 0 | 2 | 5 | 7 | 5 | 2 |
| Colonies south of 60°N (*U. aalge* + some *U. lomvia*) | 26 | 0 | 6 | 8 | 7 | 4 | 1 |

* Comparing colonies inside the limit of 10% ice cover with those outside, for colonies north of 60°, and lumping magnitudes of 4 and below and those of 5 and above, $P < 0.001$ (Fisher exact probability). Comparing colonies north of 60°, but outside the limit of 10% ice cover, with those south of 60°, $\text{Chi}^2 = 1.22$, df 1, $P > 0.2$.

**Figure 122**
Distribution of murre colonies in the western Atlantic and eastern Canadian Arctic, in relation to the occurrence of 10% ice cover during late July and the first half of August. ●, *Uria lomvia* only; ◑, *U. lomvia* & *U. aalge* mixed; ○, *U. aalge* only



(Fisher 1966, Parslow 1973). In the case of murres, despite an overwhelming tendency to return to the natal colony in all populations that have been studied (Southern *et al.* 1965, Birkhead 1977*a*), they apparently retain the ability to colonize new areas. The rapid growth of the Common Murre population at Funk Island, off eastern Newfoundland, documented by Tuck (1961) through the 1950s could probably only have occurred with the aid of immigration from other populations.

Two hypotheses can be considered regarding the origin of the present sizes and distribution of colonies in the Lancaster Sound area:

(1) that these were the first sites to be colonized, and once established attracted all subsequent immigrants to the area; and

(2) that many colonies were established initially, but only a few survived.

Although there is no evidence that colonies were ever more numerous in the area, ice conditions were probably far less severe during the post-glacial hypsithermal period [6000–4000 years B.C. (Godwin 1956, Flint 1957)] than they are now. By analogy with the situation in West Greenland we might therefore expect that more smaller colonies became established at that time. Subsequent deteriorations of climate and increasing summer ice cover would have led to strong selection against the establishment of new colonies and, perhaps, a movement from smaller to larger colonies, culminating in the present huge aggregations. Under this hypothesis the origin of the high arctic colonies, such as Prince Leopold Island, can be traced to conditions that no longer exist. They sustain themselves, through their sheer size and the flexibility that it gives them due to the information centre effect, in a situation where colonization now, starting inevitably with small numbers, would be impossible. This makes them essentially relict populations, although they are not, traditionally, regarded as such.

Three points arise from the foregoing considerations:

(1) If the present conditions have been in existence since the end of the hypsithermal period, then we may anticipate that the populations involved will have lost much of their potential to respond to changes in the normal patterns of distribution of their food resources. This is because individuals possessing any tendency to attempt breeding outside existing colonies will have been constantly selected out.

(2) Prince Leopold Island, being the most westerly colony in the Parry Channel and subject to the least predictable ice conditions, may be the most vulnerable of the high arctic colonies to events that might disrupt the present pattern of feeding areas or to minor climatic perturbations.

(3) If the size of the colony is one of the factors determining the reproductive success of constituent individuals, then there must be a critical size, in relation to the predictability of food supplies, below which the reproductive output of the colony cannot sustain the population. At this point the colony would begin an accelerating decline, leading to its eventual extinction.

Both of North America's most celebrated avian extinctions during the last 200 years, the Great Auk *Pinguinus impennis* and the Passenger Pigeon *Ectopistes migratorius*, were of species which reproduced in large aggregations and which were, prior to the advent of western man, exceedingly numerous (cf. also Halliday 1980). There are no grounds, therefore, for assuming that the present abundance of the Thick-billed Murre is a guarantee of its survival in the face of changing conditions. Its present distribution, concentrated in a few massive colonies, must make it far more vulnerable than a species such as the Black Guillemot, which nests over most of the arctic coastline.

Features of breeding at Prince Leopold Island, *left*, steep cliffs associated with predictable open water (D.N. Nettleship); *right*, ledges suitable for high density breeding (E. Greene)

## 3. Factors controlling population size

The application of Diamond's (1978) hypothesis on factors controlling the size of seabird populations to the relative abundance of species in the Lancaster Sound area depends on the assumption that populations are controlled by the availability of food during the breeding season, a theory proposed for seabirds by Ashmole (1963) and expanded by Rowan (1965). The idea is based mainly on the assumption that populations are able to forage less efficiently during the breeding season, because they are limited by the location of their colony. Outside the breeding season, however, they are free to follow important prey species wherever these are most abundant, many species crossing the equator in the process.

For Thick-billed Murres, which remain throughout the winter north of latitude 45°N where bad weather is normal rather than exceptional and daylight available for feeding is limited (Tuck 1961, Salomonsen 1972), the idea that food is more readily obtained during the winter is less attractive. However, the timing of mortality in the Common Murre (Mead 1974, Birkhead and Hudson 1977) indicates that natural adult mortality is highest where the degree of density-dependence is likely to be very small, particularly as a result of very extreme weather conditions (Fleming 1905, Tuck 1961, Bailey and Davenport 1972, Bourne 1976). Thus, density-dependent regulation during the breeding season remains a possibility.

Judging from the rather small amount of information available, murres breeding in small colonies usually forage within a few kilometres of their breeding site (Cody 1973, Wiens and Scott 1975, Ashcroft 1976, Birkhead 1976*a*), whereas those from colonies of more than 10 000 pairs normally forage over much larger areas (Chapter V, 4.5). A similar situation may exist for Northern Gannet colonies (Nelson 1978) and these observations indicate a positive correlation between colony size and foraging range.

If Thick-billed Murres from large colonies, such as that at Prince Leopold Island, travel long distances to feed, then they probably maximize their foraging efficiency by doing so, indicating that the density or accessibility of prey varies within their foraging range. The possible magnitude of such variation can be obtained from a simple model based on the assumption that the time required to catch a unit of prey is proportional to the rate of encounter and that for a bird hunting in a three-dimensional space, as murres presumably do, this is inversely proportional to the cube root of the density. Time devoted to catching prey is divided into the time spent in transit between the colony and the feeding area ($T$) and the actual time spent capturing prey in the water ($t$).

Comparing two feeding areas at different distances from the colony ($L_1$ and $L_2$, where $L_2 > L_1$), the ratio of prey densities in the two areas ($D_2/D_1$), which would make travelling to either equally profitable, can be predicted from equation [1] (App. 27),

$$[1] \qquad \frac{D_2}{D_1} = \left[ \frac{t_1}{t_1 + (NL_1 - NL_2)/S} \right]^3$$

where $S$ is the flight speed in kilometres per hour and $N$ is the number of round trips made per day.

Using the extreme case, where the nearer location is immediately adjacent to the colony, then $L_1 = 0$, and hence:

$$[2] \qquad \frac{D_2}{D_1} = \left[\frac{t_1}{t_1 - (NL_2)/S}\right]^3$$

From equation [2] we can calculate the minimum prey densities, in relation to the density adjacent to the colony, that would make it profitable for birds to travel a given distance. Figure 123 shows $(D_2/D_1)$ where $t_1 = 10$ h/day, probably close to the actual foraging time available during incubation and chick rearing, when members of breeding pairs are taking alternate 12-h shifts, leaving 2 h for social behaviour, preening, and resting. During incubation, birds probably made only one journey to the feeding area each day, so that travel time $(T_2)$ was estimated from equation [3]

$$[3] \qquad T_2 = \frac{2L_2}{S} \text{ h}$$

For the chick-rearing period, we assumed a situation in which parents were making two trips each day to their feeding area, hence doubling $T_2$.

Because of the need to return to the colony within 12 h, travel time sets an upper limit to the murres' foraging range as it approaches the total foraging time available. Under the assumptions outlined above, this limit would be 350 km during incubation and 175 km while feeding chicks. Observed foraging ranges fall well inside these limits in the case of the Prince Leopold Island colonies (Chapter V, section 4.5).

The hyperbolic shape of the curve in Figure 123 means that the difference in prey density required to make it profitable for birds to travel farther from the colony increases as they proceed outwards. For example, to make it worthwhile to travel 50 km from the colony during chick rearing, a density ratio of 2.7 is sufficient; but to make it worthwhile to continue another 50 km beyond that, up to 100 km, a density ratio of 4.6 would be necessary. Given the apparent constraints imposed by the requirements of the murre chick, the normal foraging range of Thick-billed Murres would probably not exceed 140 km during chick rearing. If the maximum foraging range of murres during chick rearing reaches a limit imposed by the need to maintain a given rate of delivery to their chicks, and assuming that the size of food items that can be carried is similar among all populations, then colony size should be related to the available area of water and the density of prey species within the foraging radius. The model outlined above can be extended to examine these relationships and their consequences.

We assume initially that the foraging radius of the colony will be related to the number of birds in the colony ($N$) and the mean density of prey ($D$) in surrounding waters. For a given mean density of prey, the area over which members of the colony forage should be equal to $N{\cdot}a$, where $a$ is a constant representing the area required to supply the foraging requirements of a single bird. If the colony is

**Figure 123**
Hypothetical relationship of the ratio of prey densities at a given distance from the colony to densities adjacent to the colony ($D_2/D_1$) that would make it profitable for Thick-billed Murres to travel that far to feed (equation [2])

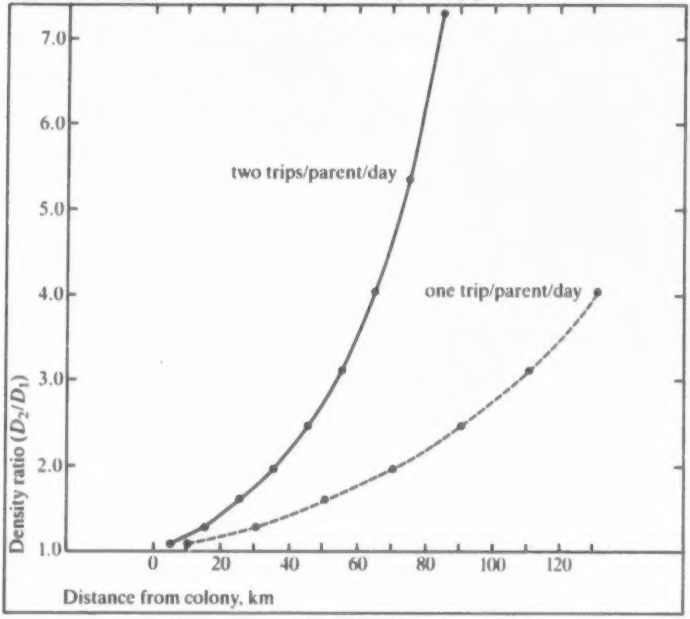
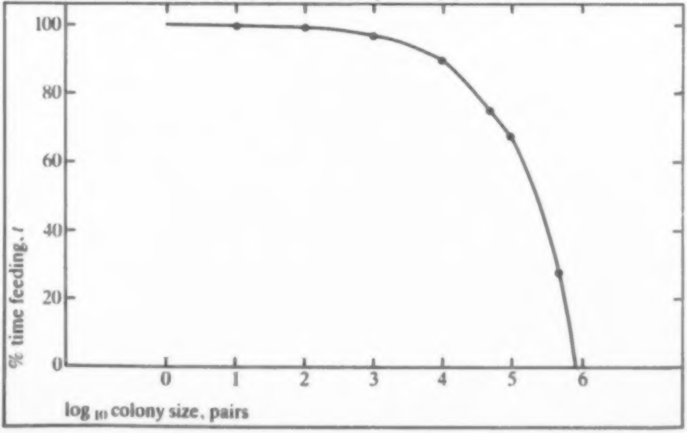


**Figure 124**
Hypothetical relationship between colony size and proportion of time available for feeding ($t$), assuming uniform prey density (equation [6], $a = 0.1$ km$^2$)



assumed to be on a small island, with seas stretching to the limits of foraging in every direction, then the maximum foraging distance ($F$) can be calculated from equation [4].

$$[4] \qquad F = (N \cdot a/\pi)^{1/2}$$

During chick rearing, when both parents make two trips a day to the feeding area, the maximum travelling time for a pair over 24 h ($T$) is then calculated from equation [5].

$$[5] \qquad T = \frac{2VF}{S} = \frac{2V \cdot (N \cdot a/\pi)^{1/2}}{S} \text{ (h)}$$

where $V$ = total number of feeding visits per chick per day. Allowing 2 h per parent for resting, preening, and other maintenance activities, the minimum feeding time available ($t$) is then calculated by equation [6].

$$[6] \qquad t = 20 - T = 20 - \left[ \frac{2V \cdot (N \cdot a/\pi)^{1/2}}{S} \right]$$

Using equation [6] and substituting an arbitrary value for $a$, we can then calculate the proportion of time available for feeding to birds from colonies of different sizes (Fig. 124). We can assume that under conditions of long-term stability colonies will expand to a size where additional travelling necessitated by increased population size is counterbalanced by decreased fledging success or post-fledging survival caused by the inability of parents to sufficiently provision their chicks. For the value of $a$ used in Fig. 124 (0.1 km$^2$), there is a theoretical upper limit to the population of about one million pairs, at which point travelling time takes up the entire 20 h available. The curve also predicts that birds from a colony the size of Prince Leopold Island will spend about 25% of their time in travelling, equivalent to a foraging radius of 44 km.

One interesting effect arising from the convex shape of the curve in Figure 124 is that a reduction in the size of large colonies will have a greater impact on foraging range than a similar reduction in the size of small colonies. The resulting density-dependent recovery would therefore be more effective for a large colony than for a small one.

The assumption of a constant density of prey within the foraging ranges of colonies of different sizes or geographic locations is clearly incorrect, if we assume that all colonies have reached an equilibrium size. Assuming that feeding time ($t$) is inversely related to the cube root of prey density ($D$), we can modify equation [6] to incorporate different relative densities. Different densities of prey affect not only feeding time, but also the area of water that can support a single bird ($a$), and $D$ therefore appears three times in equation [7] (App. 28).

$$[7] \qquad N = \pi \left\{ \frac{20S}{2V} \left[ 1 - \frac{1}{(D_x)^{1/3}} \right] \right\}^2 \cdot \frac{(D_x)^{1/2}}{a_1}$$

Using equation [7] we can construct a curve relating the size of colonies to the density of prey in surrounding waters (Fig. 125). One of the most noticeable features of that curve is that prey density has

**Figure 125**
Relationships between colony size and mean prey density in surrounding waters (solid line), and between colony size and maximum foraging radius (dashed line) (equation [7], $a = 0.1\ \text{km}^2$, $V = 4$, chick-rearing period)

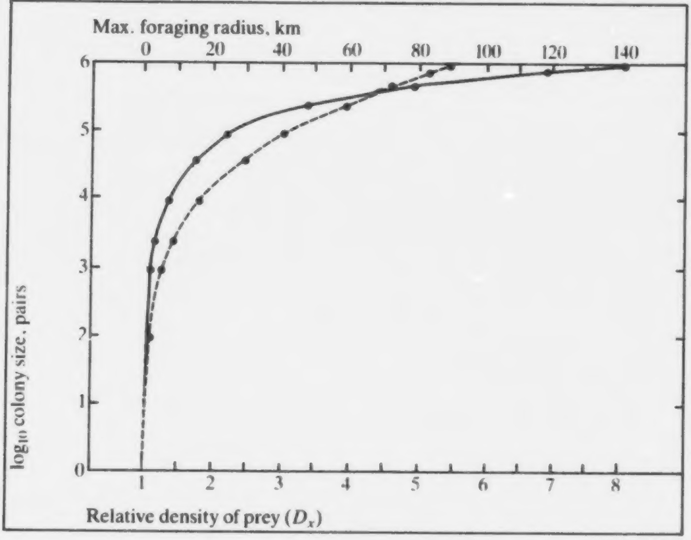
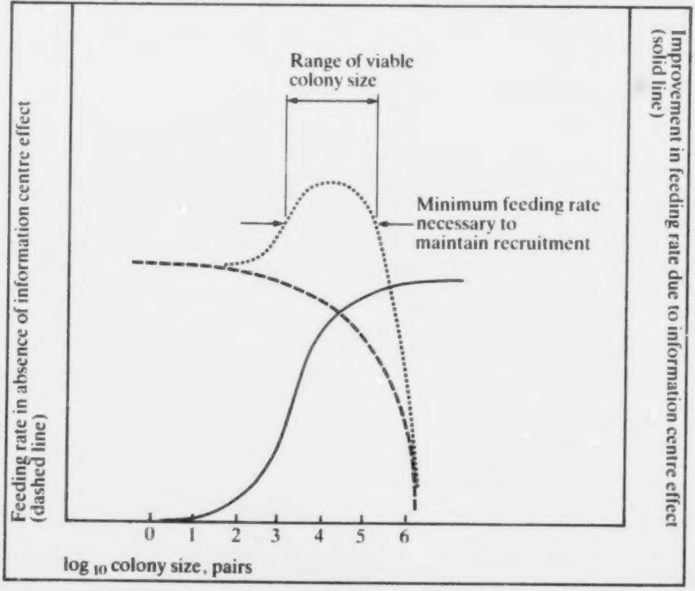


**Figure 126**
Interaction of food depletion and information centre effects in relation to colony size in an unpredictable environment



relatively little effect on colony size, up to about 10 000 pairs. Even the tenfold increase to 100 000 pairs involves only roughly doubling the density of prey, a fairly small difference compared with differences in productivity that are known to exist between different marine areas (Lorenzen 1976, Tranter 1976, Brown 1980). Although this model is very crude and makes a number of arbitrary assumptions, the overall shape of the curve is probably approximately correct. If so, then it goes some way to explain the rarity of small murre colonies, except in areas affected by human disturbance, since prey densities sufficient to support a few birds are very close to those capable of supporting thousands. It also suggests a limit to colony size at about one million pairs, a figure close to the observed limits of colony size at present (Brown *et al.* 1975).

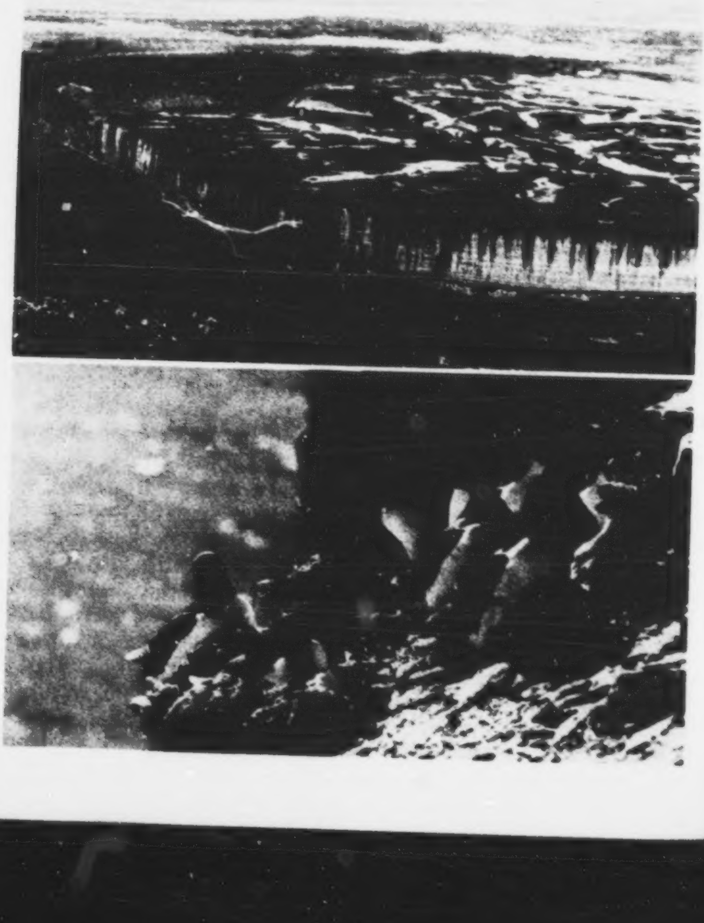
Combining the hypothesis that colony size is limited by increasing foraging range with the hypothesis that in the unpredictable arctic environment only large colonies are viable, overcoming the problem of spatial unpredictability through the information centre effect produces rather complex predictions. A decrease in colony size should result in greater availability of prey for the remaining birds, but a slower response to changes in the location of feeding areas. Modelling becomes extremely speculative at this point, because, at present, we cannot quantify the value of the information centre effect or the manner in which it relates to colony size. We can predict, however, that as colonies decrease in size in areas where the information centre effect is important, the rate of feeding of the chicks will become more erratic.

The interaction between the depletion of food resources and the information centre effect is summarized in Figure 126. Whatever the exact nature of the relationship, which is probably unique to each colony location, there is probably a range of viable colony sizes. Under natural conditions colonies should exist at the upper limit of this range, except after periods of catastrophic mortality. Reduction in numbers should lead initially to an opposite, density-dependent reaction, operating through an increase in reproductive output. If the speed of the decline is too rapid to be reversed by this process, however, and the size of the colony falls below the lower limit of viability, then the decline can be expected to continue with accelerating speed.

A density-dependent mechanism, affecting reproductive output more obviously than the supposed depletion of food supplies, can be discerned in the effects of breeding-site characteristics on breeding success. Much of the observed difference in breeding success between pairs of murres at Prince Leopold Island could be attributed to differences in the physical structure of their breeding sites (Chapter III). Assuming that competition occurs for the most suitable sites, a reduction in population should result in a rise in the proportion of pairs laying on good sites and, hence, an increase in overall breeding success for the population. After a sharp decline in numbers on a colony of Common Murres at Skomer Island, Wales, however, the remaining birds did not occupy those sites which would have resulted in the greatest breeding success (Birkhead 1977*a*). This was attributed to inertia on the part of the remaining birds which, once they had settled on a site, did not move despite better sites becoming vacant elsewhere. If the mechanism is dependent on adjustments made through the settlement patterns of young birds, it will take some time for rearrangements to occur, owing to the low rate of recruitment.

The argument that Thick-billed Murre populations are regulated by density-dependent mechanisms operating to determine reproductive output is contradicted by the levels of breeding success recorded at Prince Leopold Island, where an average of 0.75 chicks were reared per breeding pair per annum between 1975 and 1977. This level of reproductive success is more than adequate to maintain the breeding population, but mortality immediately after fledging is high (Chapter III, section 4.4) and may be related to the condition of the chicks as they leave the cliffs, which, as we have argued, may be a function of density. The type of information required for a key-factor analysis of density-dependence in Thick-billed Murres will probably not be available for a long time because of the difficulties involved in enumerating the entire population and pin-pointing the timing of mortality. However, if density-dependent regulation is occurring through adjustments in reproductive output, then such compensation should take many years to have an effect because of low recruitment and deferred maturity.

*Above*, the East Cliff colony area (D.N. Nettleship); *below*, on a seaward sloping platform, 21 August 1978 (E. Greene)



# 4. The fledging strategy of the Thick-billed Murre

The hypothesis advanced here, that travel time places a constraint on colony size, leads to the assumption that there must be constant selection pressure operating on the population to minimize the effect of travel time. There are several adaptations which could reduce this constraint: (1) increase flying speed, (2) increase the amount of food that can be carried to the chick, and (3) decrease the food requirements of the chick.

The range of level flight speeds exhibited by birds is not very great (Pennycuick 1969), which suggests that there is relatively little room for improvement in this direction. Realized ground speeds are likely to be a compromise between the maximum speed and the most economical speed for covering the distance, in terms of energy expenditure (Tucker 1968). Thick-billed Murres certainly travel considerably faster in level flight than either kittiwakes or fulmars and this is probably partly a result of their high wing-loading.

The body size and wing-loading of the murres must represent a compromise between the optimum dimensions for a pursuit-diving fish-eater and the maximum wing-loading possible without sacrificing the option of flight — an option abandoned by the penguins and the extinct Great Auk, birds that resemble murres in their feeding behaviour. Adaptation to a very high wing-loading has inevitably reduced the ability of murres to transport additional weight and hence limited their capacity to provision their chicks. The amount of food carried in a single load by adults feeding chicks is smaller, in proportion to body weight, for the large alcids (*Uria, Alca*) than for the smaller ones (Cody 1973). This may be a simple allometric effect of selection for larger body size.

Chicks can adapt to a decrease in the rate at which they are fed either by reducing their rate of growth or by developing the ability to fledge at a lower weight. The genus *Uria*, in which chicks fledge at 20–25% of adult body weight (two to three times fresh egg weight), is intermediate in fledging strategy between the fully precocial, nidifugous murrelets of the genera *Endomychura* and *Synthliboramphus* and the semi-precocial, nidicolous Atlantic Puffins, Black Guillemots, and most other alcids, in which the young fledge at close to adult weight. A general consensus is that the murres have adopted this fledging strategy because the adults are incapable of rearing their chicks to full adult weight on the breeding site (e.g., Greenwood 1964, Lack 1968, Sealy 1972, Cody 1973, Scott 1973, Birkhead 1977*b*). We believe that this adaptation, being a byproduct of the adult's increased feeding efficiency, constitutes a classical *K*-selected strategy, trading reduced reproductive success for increased adult survival.

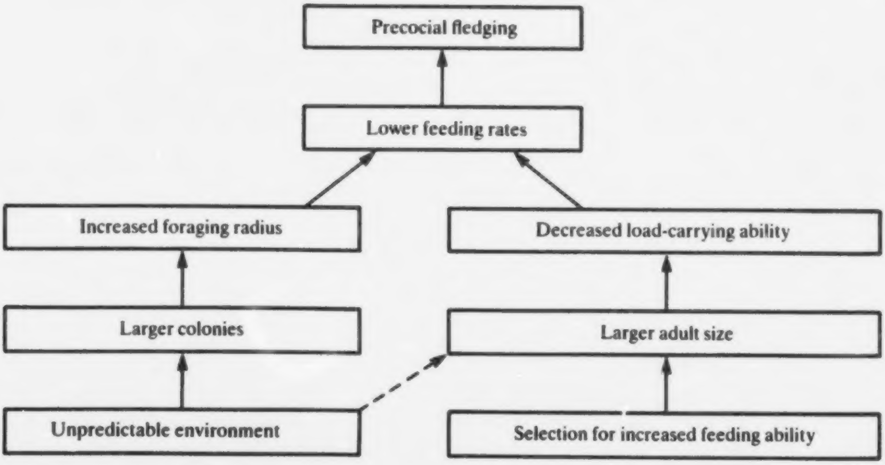
The decrease in the amount of time invested in provisioning their chicks, which Thick-billed Murres derive as a result of their fledging strategy, is demonstrated by a comparison with another pursuit-diving fish-eater, the Double-crested Cormorant *Phalacrocorax* *auritus*. In the cormorant, parent birds double their foraging effort during chick rearing to rear three or four young (Dunn 1975). In contrast, even with the rather optimistic assumptions made in Chapter IV, section 4.3, Thick-billed Murre parents add no more than an extra 20% to their normal foraging budget during chick rearing.

The selection pressures toward precocial behaviour in chicks become greater with increasing colony size, because of the increased amount of time spent travelling. Under arctic conditions, therefore, with only very large colonies able to survive, the pressures towards precocial fledging must be particularly acute. Figure 127 summarizes some of the factors which are important in the evolution of the murres' fledging strategy.

*K*-selected life-history strategies are common to practically all offshore-feeding seabirds, all of which must spend long periods of time travelling between feeding grounds and breeding sites (Lack 1968). Among surface-feeding and plunge-diving species, however, which spend most of their time in flight while foraging, precocial fledging is impossible because the flightless chicks would be unable to accompany their parents. Instead, many of these birds have evolved extended fledging periods and the capacity for the adults to carry large food loads, a strategy taken to its furthest extreme in the Procellariiformes.

In some respects the adoption of a *K*-selected strategy in response to an unpredictable climate seems to contradict accepted ideas on the conditions for *K*-selection. However, *K*-selection can be expected to operate most intensively in situations where the opportunities for reproduction are unpredictable, but adult survival is high (Schaffer 1974). If the observed variation in chick fledging weights is reflected in large year-to-year differences in subsequent survival, then this condition is probably met in the case of the Thick-billed Murre.

**Figure 127**
The interrelationship of factors leading towards precocial fledging behaviour in the genus *Uria*


Precocial fledging
Lower feeding rates
Increased foraging radius
Decreased load-carrying ability
Larger colonies
Larger adult size
Unpredictable environment
Selection for increased feeding ability

# 5. The structure of the colony

A recurrent theme in our investigations was the extent and significance of diversity within the colony: in behaviour, in breeding success, in egg size and colour, and in chick feeding rates and growth rates. It was important to establish the limits of variability within the colony before attempting to interpret our results or generalize them. A colony the size of Prince Leopold Island compresses into a few kilometres of cliff a population of birds which, if breeding solitarily, might extend over a considerable geographic area. We may therefore expect variation between different parts of the colony equivalent to that occurring between local sub-populations of terrestrial birds many kilometres apart.

Some of the variation observed is determined by the structure of the breeding cliffs. The physical characteristics of the laying site play a major role in determining breeding success and, because certain types of site tend to cluster together on the cliff, this creates local unevenness in the distribution of reproductive output. The effects of various site characteristics on breeding success operate at different stages in the breeding cycle. Thus, sites particularly prone to snow accumulation may fare badly in late snowfalls and lose a high proportion of first eggs; sites vulnerable to gull predation may suffer throughout the season, but perhaps more in seasons when the nearby Glaucous Gulls are successful in rearing young; and those having poor access to the sea may lose chicks at fledging. A realistic assessment of the relative value of different types of site can only be based on monitoring reproductive success for several seasons.

The nature of the cliff may also be important in determining certain aspects of behaviour. Consistent differences in the ratio of counts to breeding pairs between different study plots suggest that the proportion of prospecting birds varies. Prospectors tend to land on broad ledges away from breeding birds. Where ledges are narrow they are unable to stay long without eliciting aggression from site-holders and hence rates of arrival and departure are high, as are the numbers of aggressive interactions.

Differences in feeding rates and chick growth rates are unlikely to be affected by characteristics of the breeding site and presumably relate to the foraging abilities of the parents, which are probably determined by their previous experience. We obtained no clear evidence on whether birds from the same part of the colony tended to forage in the same area. If they do not, then local variation in feeding rates may relate to differences in the age structure of different parts of the colony. Such diversity must arise every time there is a major cliff fall, exposing new areas of ledges for colonization. These areas can be expected to support a high proportion of inexperienced breeders initially, forming an even-age cohort for many years.

We found no evidence for Tuck's (1961) idea that young inexperienced birds settle on the fringes of the colony. His suggestion presupposes that birds gradually move towards the centre of the colony as they grow older, but what evidence there is suggests that murres display a very high level of site tenacity once they have succeeded in breeding. Young birds probably occupy any vacant site within the colony, especially those close to their natal area. Because birds often desert an unsuccessful site the next year, many sites occupied by birds breeding for the first time are suboptimal and this compounds their generally low breeding success.

The local concentration of certain types of egg colour and markings can most easily be explained if we assume a closer-than-average "relatedness" among neighbouring birds, presumably because young birds tend to return close to their natal site. The scale of this genetic effect and its expression in characters other than egg colour is hard to judge from our observations, but it cannot be ignored. The relationship between egg colour and volume indicates that genetic diversity may extend to characters having an effect on reproductive success.

Nor can the polymorphism of eggs and chicks be related solely to recognition by the adults. Adults recognize their own eggs partly by their location on the cliff and beyond a certain radius visual recognition is inoperative (Tschanz 1959). The fact that similar eggs tend to occur side by side obviously reduces the effectiveness of polymorphism for visual recognition. The plumage polymorphism of chicks seems unlikely to relate to recognition, because the majority of chicks are the same in any case and because recognition is apparently based on calls. These variations may reflect, rather, an underlying genetic diversity in the population that is characteristic of many arctic birds, including jaegers *Stercorarius* (Davis and O'Donald 1976), Ross' Geese *Chen rossii* (Williamson 1957), and Northern Fulmars (Fisher 1952), and also of arctic marine invertebrates (Dunbar 1970). Heterogeneity may be maintained by climatic instability, resulting in drastic variation in the selection coefficients for certain gene combinations between years and producing ecosystems showing a low level of between-species diversity, but high levels of within-species diversity.

The colony can, therefore, be regarded as a mosaic of different patterns of diversity; patterns of age distribution and genetic diversity are superimposed on the pre-existing variation in the cliffs themselves and the breeding sites that they provide. This is a situation that must be constantly changing as certain parts of the colony grow older and others are occupied by influxes of new breeders. Areas of particularly successful breeding sites will tend to export populations to less suitable parts of the colony, altering the overall distribution of genotypes, and the accumulation of faeces and food remains on certain ledges may gradually alter their character, causing shifts in population.

The dynamic processes in surrounding water bodies should constantly alter the balance of recruitment and mortality, causing natural fluctuation in population levels and perhaps altering the relative suitability of different colony locations. In an evolutionary perspective, our 3-year study of the Prince Leopold Island colony covers a minute fraction of the life-span of such a "superorganism", which may have already been in existence for several thousand years. Practically every seabird colony in the North Atlantic, perhaps the world, is undergoing massive changes in population related to human activities, and the result of these human-induced fluctuations is to mask natural population changes in response to changes in marine ecosystems. It is a sad commentary on our progress that even in the remote wildness of

Lancaster Sound we cannot observe the natural dynamics of a seabird colony because numbers have almost certainly declined in response to human activities, causing increased mortality in the wintering areas of the population (Nettleship 1977*a*).

What becomes evident from a consideration of the study as a whole is the interrelatedness of all the phenomena observed. The key to the entire system rests in the distribution and abundance of food, influencing every feature of the colony, from historical events such as its location and size, through inter-year differences in numbers of birds at the colony, timing of breeding, adult weights, egg volumes and growth rates, to day-to-day fluctuations in attendance patterns and feeding rates. Unfortunately, it is the distribution and abundance of food that we know least about; the role of food supplies, in most cases, being inferred only from circumstantial evidence.

Because of the ubiquitous influence of food supplies on all aspects of the murre's breeding biology, we cannot consider any one aspect as independent of another. Reproductive success, for example, may be influenced by the availability of food through its effect on the timing and synchrony of laying, the proportion of site-holders laying, the size of eggs, the amount of aggression caused by the presence of prospecting birds, and the growth of chicks. If a larger proportion of young, inexperienced birds breed in a year when food is abundant, using mainly suboptimal sites, then this may cause a lower mean reproductive success per pair, but a higher gross productivity for the colony.

To demonstrate relationships within such a closely-knit system is not difficult, but assigning a relative magnitude to the different effects operating on any single phenomenon becomes almost impossible, particularly when the most important determinant, the availability of food, is extremely difficult to measure. What we have achieved in this study is merely to lay the groundwork for an understanding of the breeding ecology of the Prince Leopold Island murres. A true appreciation of the mechanisms governing the operation of such a colony awaits an investigation which integrates knowledge of events at the colony with detailed monitoring of changes in the distribution and abundance of the murre's principal prey organisms.

# 6. Summary

(1) There are few species of seabird in Lancaster Sound, relative to seabird communities at lower latitudes.

(2) The relative abundance of breeding birds on Prince Leopold Island reflects their relative abundance in the Lancaster Sound region as a whole, with Thick-billed Murres being the most numerous species in both cases. Relative abundance may be related to the volume of water available to each species for foraging.

(3) Arctic cod are of major importance in the diet of chicks and probably adults of the three most abundant seabird species breeding in the Lancaster Sound region and this fish plays a pivotal role in the marine food web.

(4) The adaptive significance of the very large colonies which contain most of the western Atlantic population of Thick-billed Murres may be partly explained by the "information centre" effect. If this is true, then a serious depletion of numbers could lead to reduced breeding success for the remaining population, and this has serious implications for conservation.

(5) The assumption that murre populations are limited by the availability of food during chick rearing leads to predictions regarding the maximum viable size of colonies and the relative densities of prey supporting colonies of different sizes. A model incorporating the idea of the information centre effect suggests that for any given colony location there is a range of colony size within which individual reproduction can be successfully maintained, but that there may be both upper and lower limits.

(6) The semi-precocial fledging of murre chicks is regarded as an example of a *K*-selected adaptation and the concentration of murres in large colonies is probably one of the factors causing this selection.

(7) Within the colony, breeding success and its components are determined by a complex combination of different effects, including variations in age-structure, genetic heterogeneity, and the distribution of different types of laying site. The resulting mosaic can only be effectively monitored by selecting a variety of study plots scattered throughout the colony.

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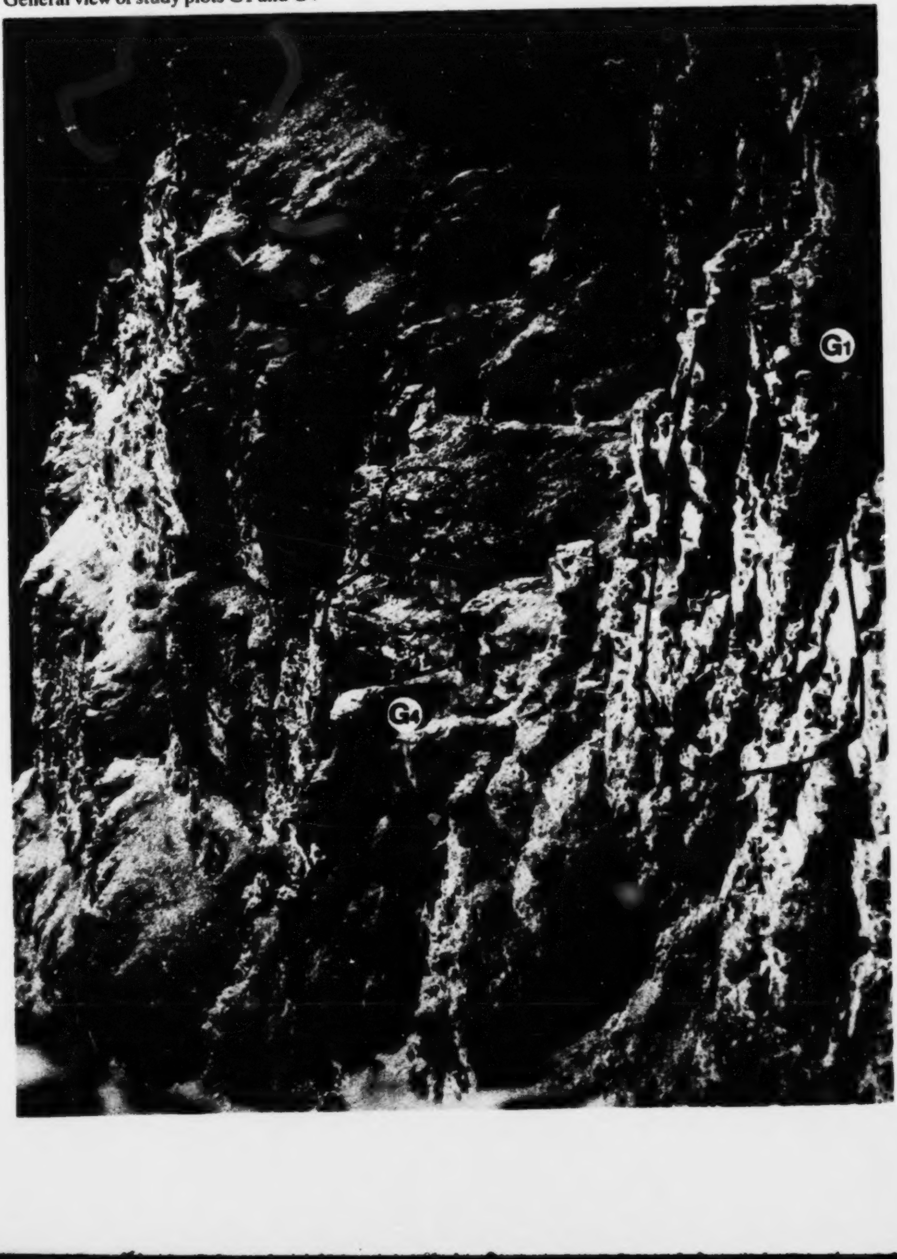
# Appendices

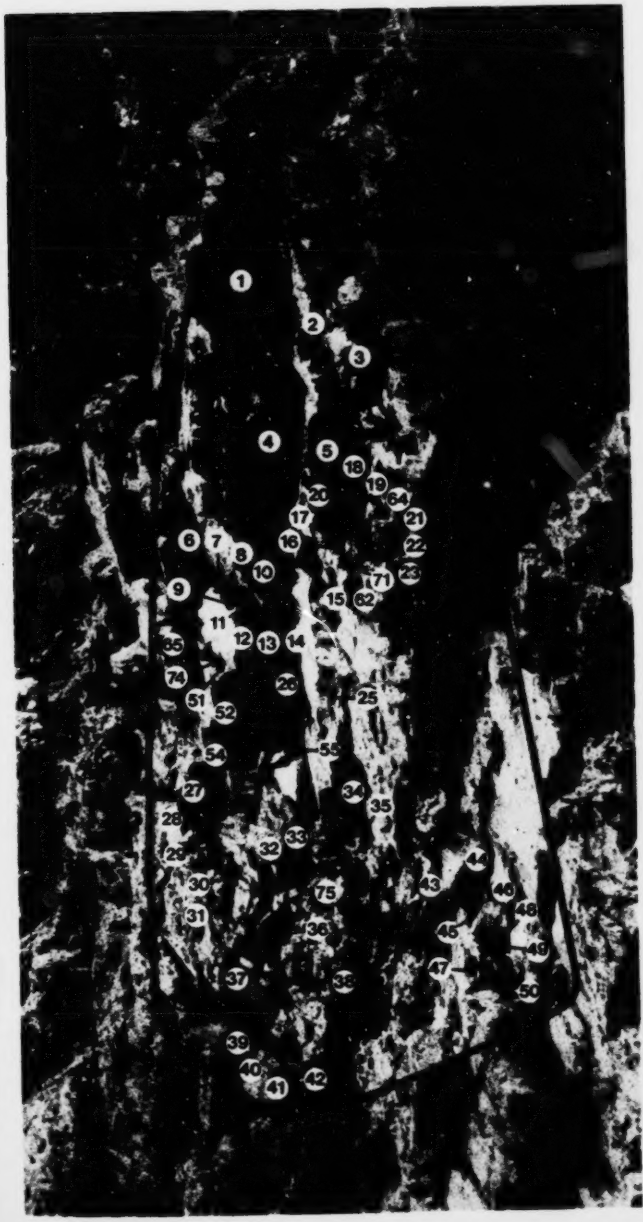
## Appendix 1

Study plot photos showing plot boundaries and positions of breeding pairs of Thick-billed Murres within each of the major study plots monitored from 1975 to 1977: G1, G4, N, Q1, Q4, S1, and U

General view of study plots G1 and G4



Close up of study plot G1 showing location of breeding sites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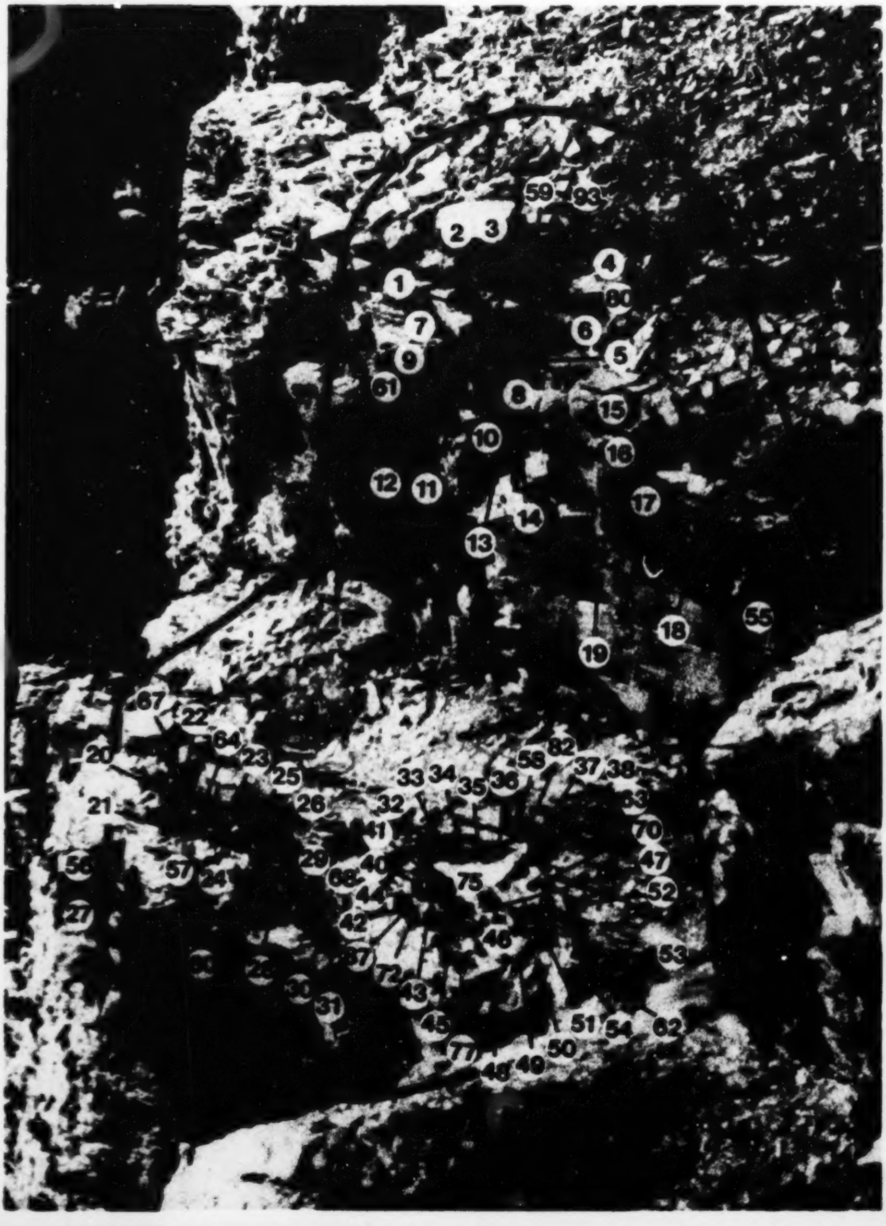
Close up of study plot G4 showing location of breeding sites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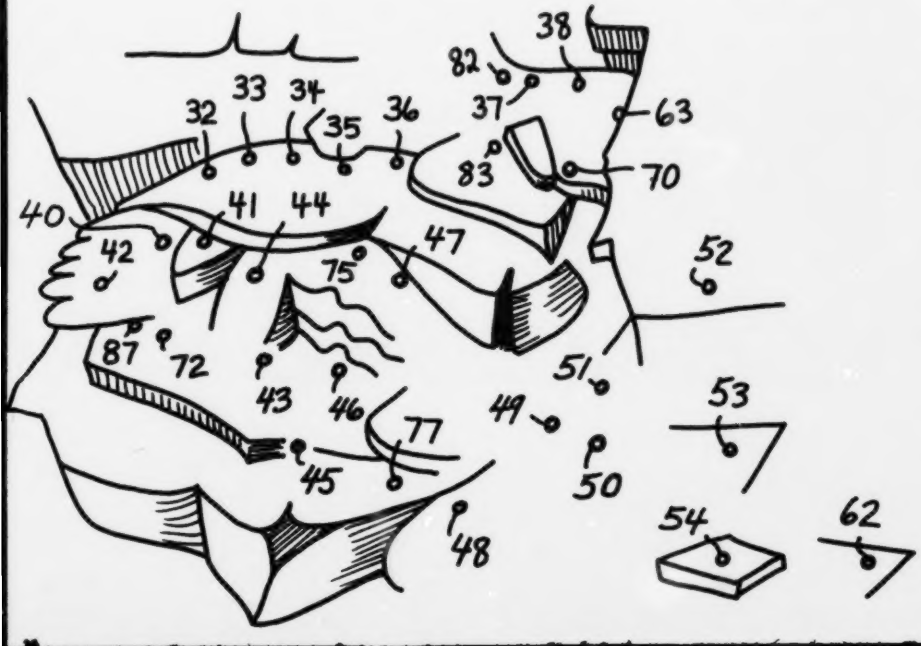
## Sketch map of study plot G4

Birds often bred so densely at some study plots that we could not rapidly locate individual breeding sites, even though we had become familiar with the general location and structure of the plot. In those instances, we drew and used sketch maps of the plots in conjunction with the plot photo. On the maps we exaggerated useful reference points — certain cliff features or landmarks — which were not as noticeable on the photos. Sketch maps for all or parts of some study plots follow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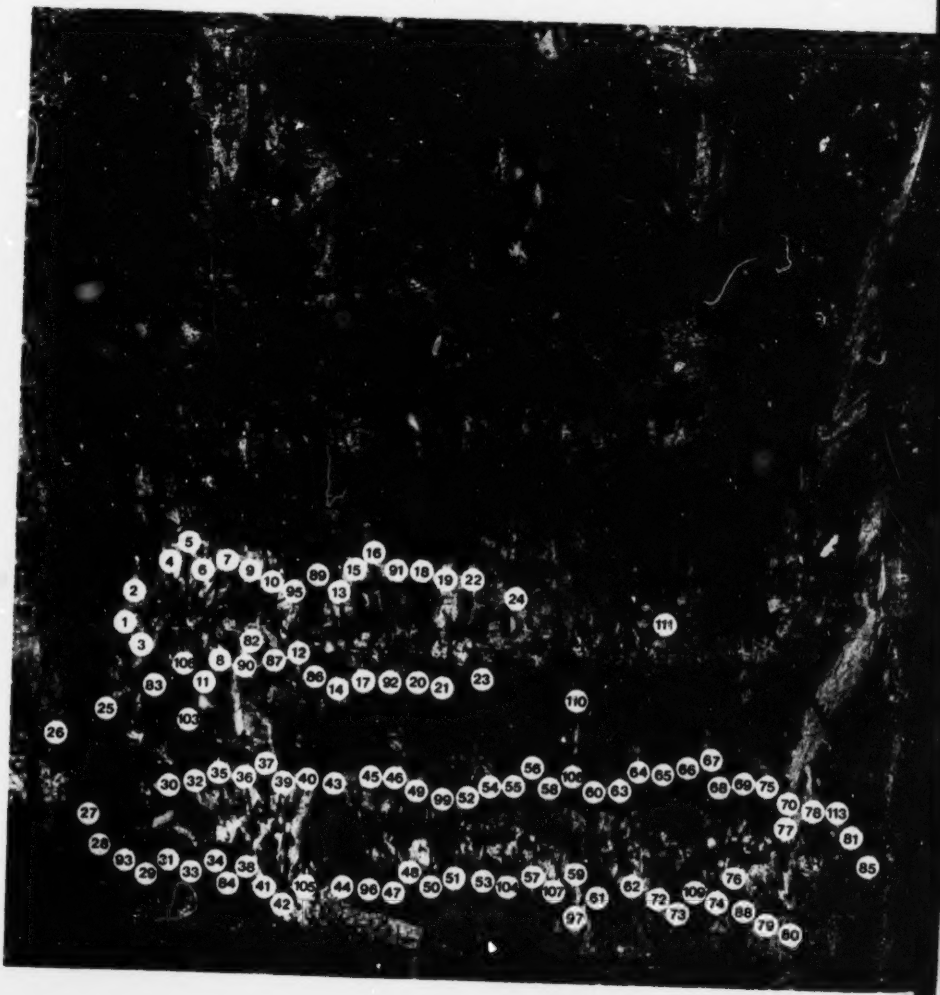
**Close up of study plot N showing location of breeding sites**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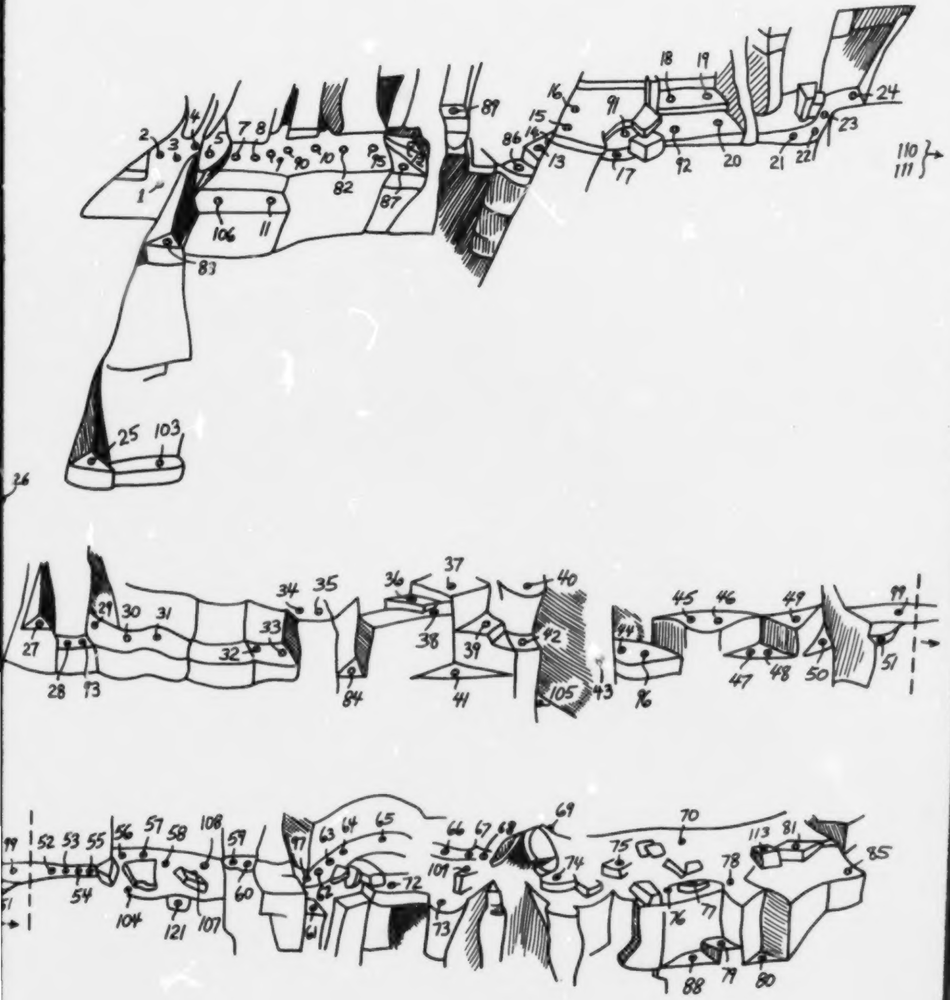
## Sketch map of study plot N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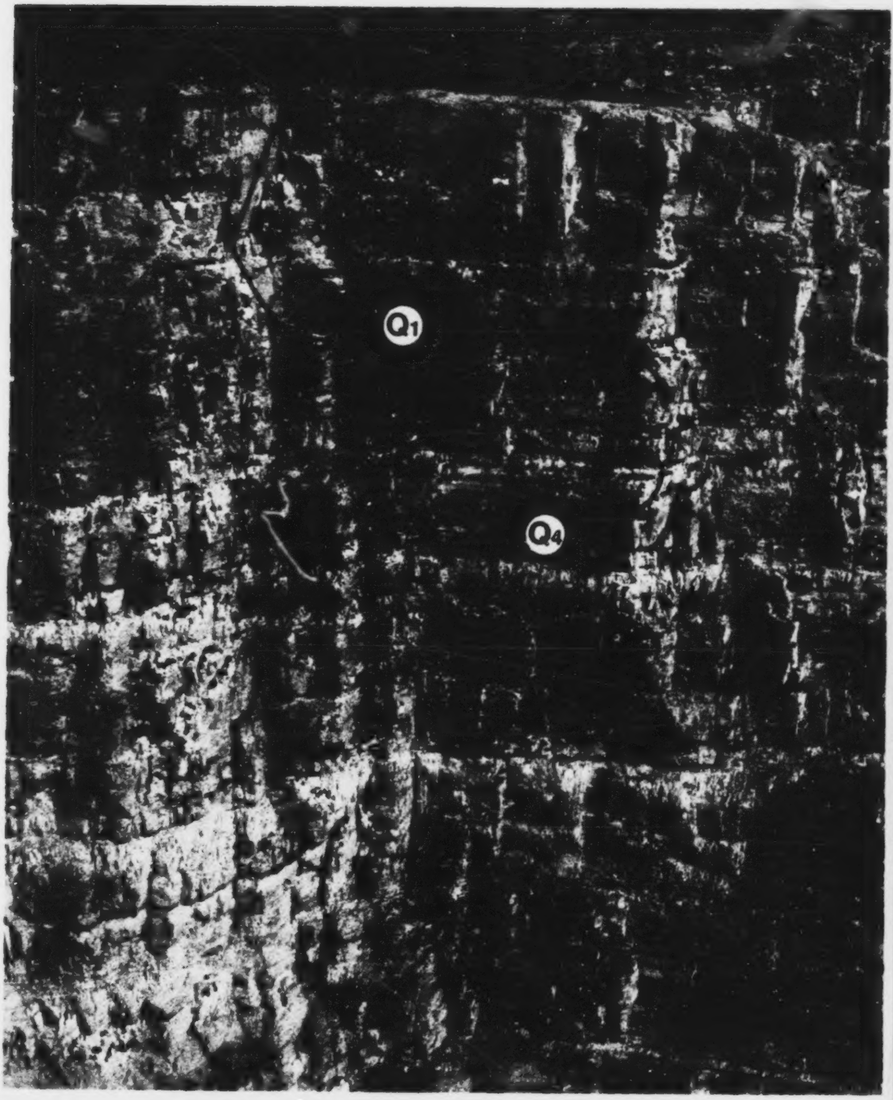
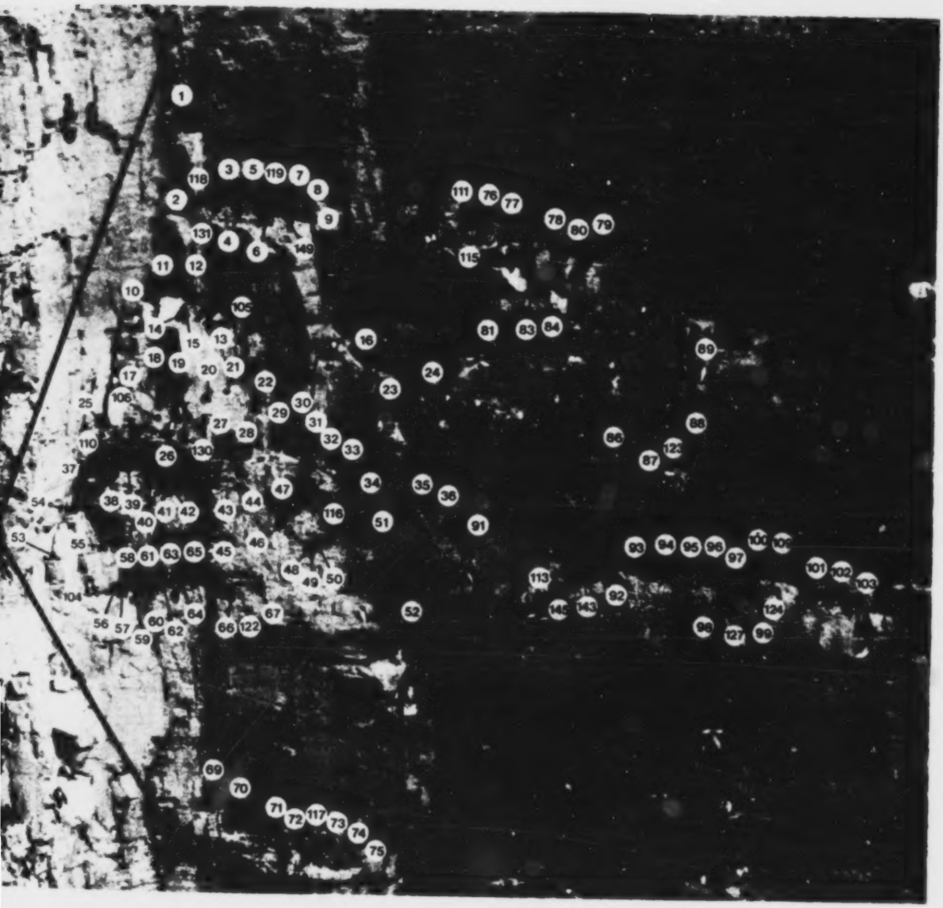
General view of study plots Q1 and Q4



Close up of study plot Q1 showing location of breeding sites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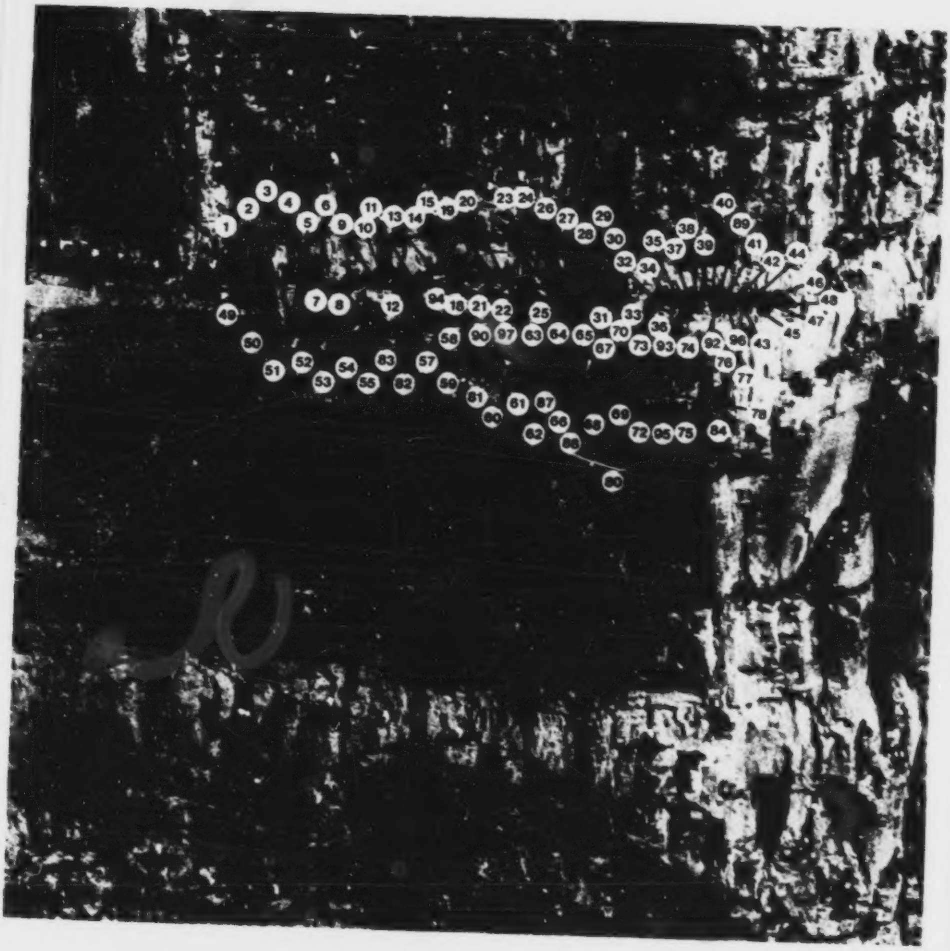
Close up of study plot Q4 showing location of breeding sites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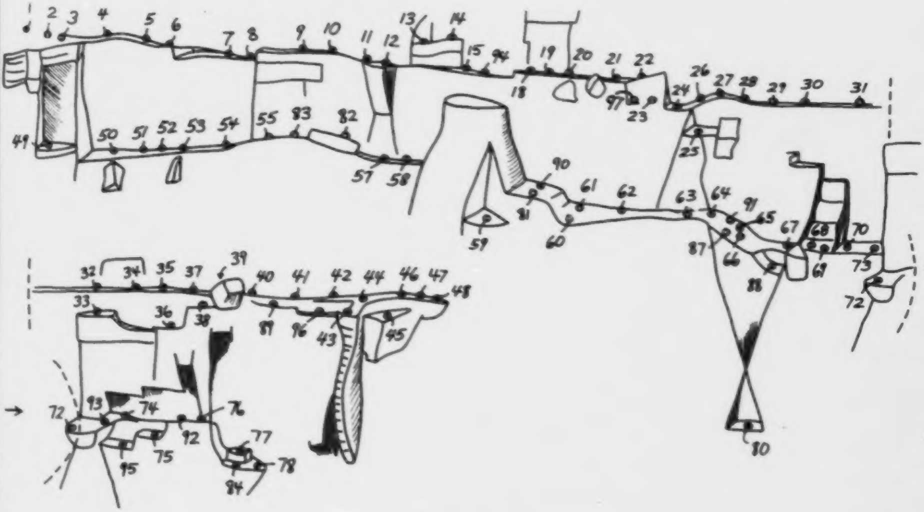
## Sketch map of study plot Q4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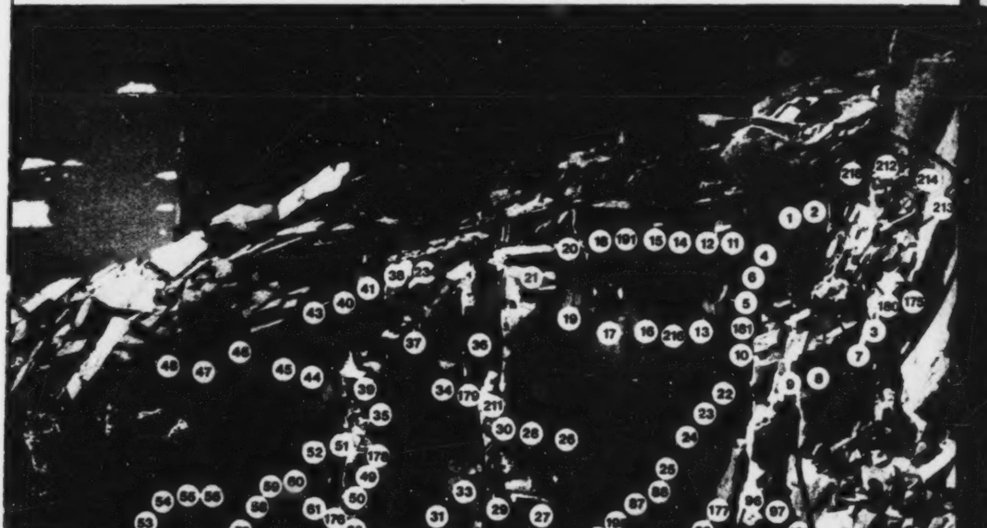
Close up of study plot S1 showing location of breedings sites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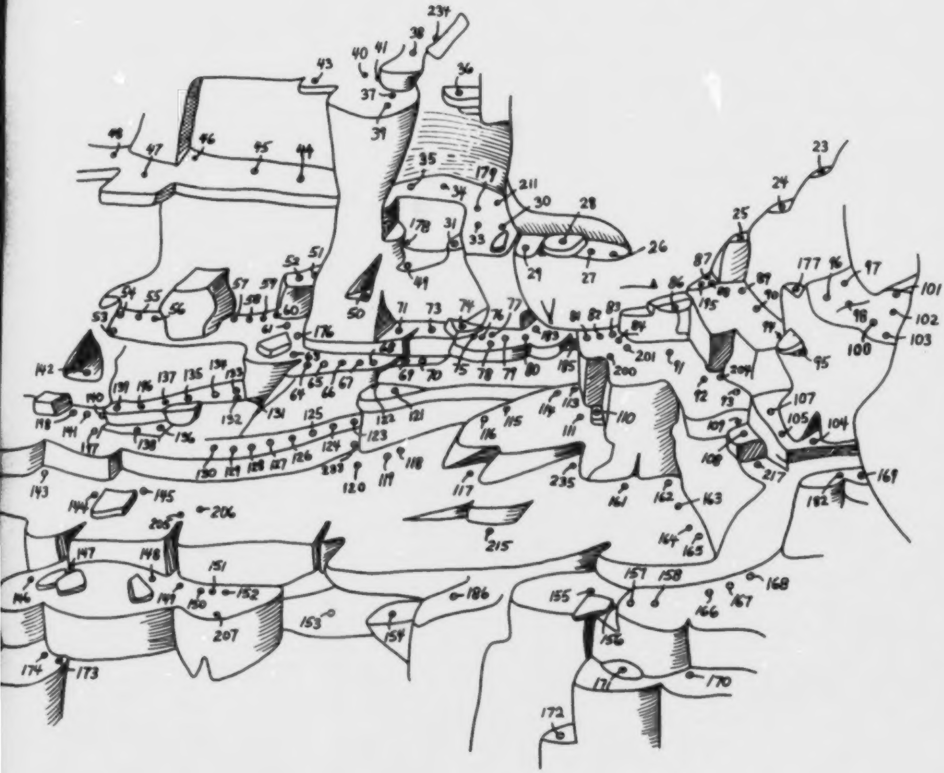
Arrows indicate sites are present in numerical sequence between the two numbers, but are not shown individually due to lack of space.

Sketch map of study plot S1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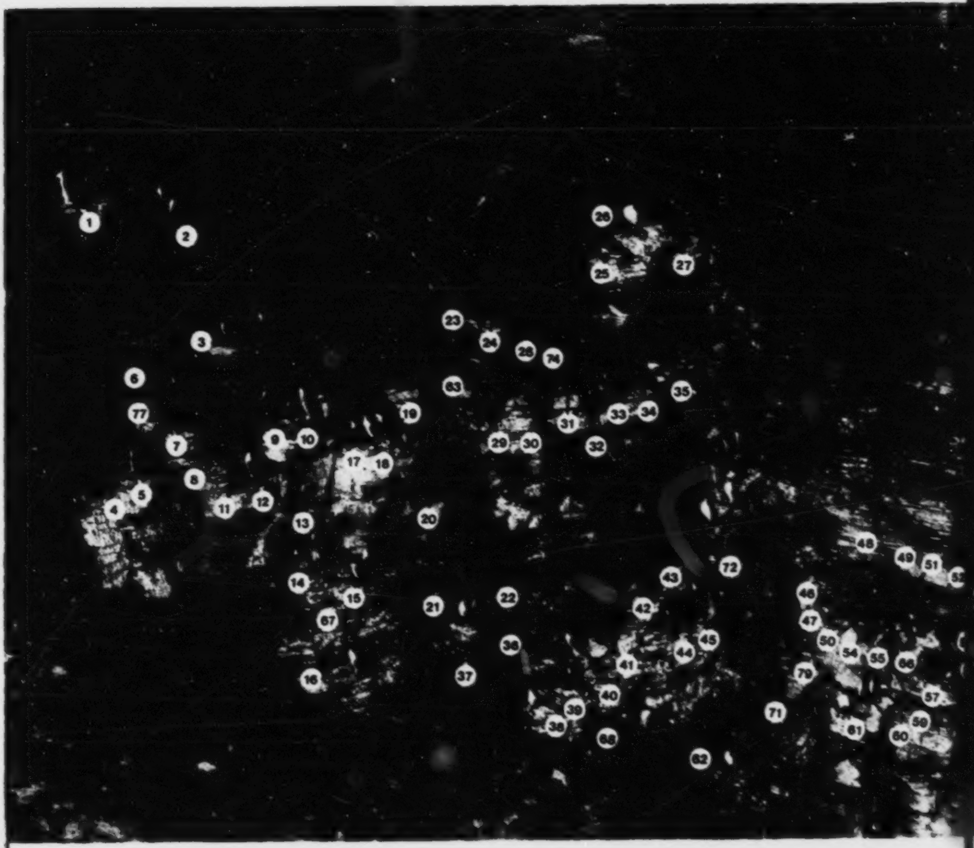
Close up of study plot U showing location of breeding sites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**Appendix 2**
Some climatic data collected during the summer months (May – September) at Prince Leopold Island, 1975–77

| | Air temp., °C | | | Wind speed, km/h | | | Wind direction* | | Barometric pressure, mb† | | Visibility,‡ km | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | 0700 | 1900 | 0700 | 1900 |
| 1975: | | | | | | | | | | | | |
| 21 May | −10 | −5 | −7.5 | 22.0 | 28.0 | 25.0 | SE | S | — | — | 8.0 | 0.2 |
| 22 | −5 | −1 | −3.0 | 8.0 | 9.0 | 8.5 | S | NE | — | — | 0.2 | 40.0 |
| 23 | −4 | −5 | −4.5 | 17.6 | 8.0 | 12.8 | NNE | NW | — | — | 40.0 | 40.0 |
| 24 | −7 | −3 | −5.0 | 14.4 | 19.2 | 16.8 | SSW | SSE | — | — | 0.2 | 0.2 |
| 25 | −3 | 0 | −1.5 | 19.2 | 1.6 | 10.4 | SSE | NE | — | — | 0.2 | 0.8 |
| 26 | −2 | −2 | −2.0 | 11.2 | 22.4 | 16.8 | SE | E | — | — | 8.0 | 0.2 |
| 27 | −2 | −1 | −1.5 | 16.0 | 36.8 | 26.4 | NE | SSE | — | — | 0.2 | 40.0 |
| 28 | −1 | 1 | 0.0 | 16.0 | 16.0 | 16.0 | E | ENE | — | — | 40.0 | 40.0 |
| 29 | 0 | 4 | 2.0 | 11.2 | 8.0 | 9.6 | E | ENE | — | — | 40.0 | 40.0 |
| 30 | 4 | 0 | 2.0 | 4.8 | 28.8 | 16.8 | ENE | NE | — | — | 40.0 | 16.0 |
| 31 | 0 | 0 | 0.0 | 24.0 | 30.4 | 27.2 | NNE | NNE | — | — | 24.0 | 40.0 |
| 1 June | 0 | −1 | −0.5 | 27.2 | 25.6 | 26.4 | NE | NE | — | — | 16.0 | 1.2 |
| 2 | −2 | −2 | −2.0 | 24.0 | 32.0 | 28.0 | NE | NE | — | — | 0.4 | 0.4 |
| 3 | −1 | −1 | −1.0 | 40.0 | 22.4 | 31.2 | NNE | NNE | — | — | 0.4 | 0.2 |
| 4 | 1 | 0 | 0.5 | 25.6 | 22.4 | 24.0 | ENE | WNW | — | — | 3.2 | 24.0 |
| 5 | 0 | 4 | 2.0 | 16.0 | 8.0 | 12.0 | S | S | — | — | 40.0 | 40.0 |
| 6 | 1 | 1 | 1.0 | 9.6 | 6.4 | 8.0 | SE | S | — | — | 40.0 | 8.0 |
| 7 | 3 | 4 | 3.5 | 6.4 | 3.2 | 4.8 | SE | NNE | — | — | 0.4 | 16.0 |
| 8 | 3 | 4 | 3.5 | 3.2 | 6.4 | 4.8 | SE | NNE | — | — | 4.8 | 40.0 |
| 9 | 2 | 2 | 2.0 | 16.0 | 28.8 | 22.4 | WNW | N | — | — | 16.0 | 0.8 |
| 10 | 0 | 1 | 0.5 | 20.8 | 24.0 | 22.4 | WNW | WNW | — | — | 0.8 | 40.0 |
| 11 | 0 | 4 | 2.0 | 12.8 | 6.4 | 9.6 | WNW | N | — | — | 40.0 | 40.0 |
| 12 | 0 | 0 | 0.0 | 6.4 | 25.6 | 16.0 | WSW | SE | — | — | 0.8 | 0.4 |
| 13 | 0 | 3 | 1.5 | 20.8 | 4.8 | 12.8 | WNW | SSE | 10.5 | 16.2 | 0.4 | 40.0 |
| 14 | 2 | 7 | 4.5 | 9.6 | 19.2 | 14.4 | WNW | W | 18.5 | 21.8 | 0.4 | 40.0 |
| 15 | 7 | 9 | 8.0 | 4.8 | 6.4 | 5.6 | SSW | WSW | 23.3 | 23.2 | 40.0 | 40.0 |
| 16 | 10 | 9 | 9.5 | 4.8 | 8.0 | 6.4 | WSW | SSW | 25.1 | 23.6 | 40.0 | 40.0 |
| 17 | 8 | 2 | 5.0 | 17.6 | 27.2 | 22.4 | W | NNW | 20.2 | 20.2 | 40.0 | 40.0 |
| 18 | −2 | 1 | −0.5 | 27.2 | 17.6 | 22.4 | NNW | SW | 18.8 | 14.6 | 0.2 | 4.8 |
| 19 | 0 | −1 | −0.5 | 35.2 | 28.8 | 32.0 | NW | W | 10.8 | 10.9 | 0.2 | 0.4 |
| 20 | −1 | 2 | 0.5 | 17.6 | 4.8 | 11.2 | W | SE | 11.1 | 09.2 | 0.4 | 1.6 |
| 21 | 0 | −1 | −0.5 | 24.0 | 48.0 | 36.0 | E | NE | 04.2 | 03.8 | 40.0 | 0.8 |
| 22 | −1 | 3 | 1.0 | 33.6 | 14.4 | 24.0 | ENE | NW | 06.0 | 09.3 | 0.4 | 16.0 |
| 23 | 4 | 3 | 3.5 | 19.2 | 19.2 | 19.2 | NNW | NNW | 11.2 | 13.2 | 32.0 | 32.0 |
| 24 | 4 | 8 | 6.0 | 3.2 | 12.8 | 8.0 | S | N | 13.8 | 14.1 | 32.0 | 40.0 |
| 25 | 6 | 9 | 7.5 | 12.8 | 19.2 | 16.0 | NNE | NW | 15.2 | 15.0 | 40.0 | 40.0 |
| 26 | 6 | 7 | 6.5 | 16.0 | 40.0 | 28.0 | NW | N | 15.2 | 16.4 | 40.0 | 40.0 |
| 27 | 4 | 7 | 5.5 | 43.2 | 56.0 | 49.6 | NW | NW | 13.8 | 11.8 | 40.0 | 40.0 |
| 28 | 8 | 13 | 10.5 | 36.8 | 8.0 | 22.4 | NW | NW | 12.0 | 09.2 | 40.0 | 40.0 |
| 29 | 6 | 3 | 4.5 | 12.8 | 9.6 | 11.2 | W | NNW | 06.7 | 05.8 | 1.6 | 0.8 |
| 30 | −1 | 1 | 0.0 | 38.4 | 41.6 | 40.0 | NW | NW | 03.8 | 06.2 | 0.2 | 32.0 |
| 1 July | 1 | 4 | 2.5 | 38.4 | 30.4 | 34.4 | N | NNW | 06.6 | 06.3 | 1.6 | 40.0 |
| 2 | 7 | 8 | 7.5 | 8.0 | 28.8 | 18.4 | N | NNW | 06.6 | 08.0 | 40.0 | 40.0 |
| 3 | 3 | 6 | 4.5 | 20.8 | 17.6 | 19.2 | NW | NNW | 07.0 | 05.0 | 0.2 | 40.0 |
| 4 | 5 | 6 | 5.5 | 11.2 | 8.0 | 9.6 | N | NNE | 03.8 | 04.6 | 32.0 | 9.6 |
| 5 | 2 | 3 | 2.5 | 6.4 | 9.6 | 8.0 | SSE | W | 01.8 | 95.8 | 0.2 | 0.2 |
| 6 | −1 | 2 | 0.5 | 27.2 | 17.6 | 22.4 | NW | NW | 96.2 | 99.1 | 0.2 | 16.0 |
| 7 | 1 | 4 | 2.5 | 25.6 | 28.8 | 27.2 | N | NW | 01.8 | 06.3 | 16.0 | 40.0 |
| 8 | 1 | 3 | 2.0 | 27.2 | 11.2 | 19.2 | NW | W | 10.9 | 14.8 | 16.0 | 40.0 |
| 9 | 0 | 4 | 2.0 | 33.6 | 6.4 | 20.0 | NNW | SSW | 16.0 | 17.0 | 1.2 | 40.0 |
| 10 | 0 | 2 | 1.0 | 14.4 | 27.2 | 20.8 | SW | NW | 11.2 | 07.2 | 0.2 | 0.2 |
| 11 | 0 | 0 | 0.0 | 22.4 | 35.6 | 29.0 | NW | NW | 02.2 | 00.3 | 8.0 | 0.2 |
| 12 | 1 | 4 | 2.5 | 14.4 | 27.2 | 20.8 | NNW | NNW | 01.1 | 03.2 | 8.0 | 40.0 |
| 13 | 1 | 1 | 1.0 | 27.2 | 38.4 | 32.8 | NNW | NNW | 05.0 | 04.3 | 40.0 | 8.0 |
| 14 | −1 | 5 | 2.0 | 46.4 | 41.6 | 44.0 | NNW | N | 02.1 | 00.8 | 8.0 | 24.0 |
| 15 | 2 | 1 | 1.5 | 28.8 | 43.2 | 36.0 | N | NNE | 04.4 | 99.6 | 8.0 | 8.0 |
| 16 | −1 | 0 | −0.5 | 30.4 | 0.0 | 15.2 | NNW | — | 93.0 | 91.2 | 0.4 | 0.4 |
| 17 | −1 | 2 | 0.5 | 24.0 | 22.2 | 23.1 | NNE | NE | 89.4 | 93.6 | 0.4 | 16.0 |
| 18 | 2 | 5 | 3.5 | 0.0 | 30.4 | 15.2 | — | NNW | 96.9 | 96.2 | 40.0 | 40.0 |
| 19 | 1 | 3 | 2.0 | 33.6 | 48.0 | 40.8 | N | N | 93.3 | 91.4 | 24.0 | 40.0 |
| 20 | −1 | 0 | −0.5 | 38.4 | 9.6 | 24.0 | NW | E | 90.3 | 92.8 | 0.2 | 0.8 |
| 21 | −1 | −1 | −1.0 | 9.6 | 9.6 | 9.6 | S | SE | 99.8 | 98.0 | 0.2 | 0.4 |
| 22 | 0 | 2 | 1.0 | 22.4 | 16.0 | 19.2 | E | NE | 01.6 | 04.4 | 8.0 | 0.8 |

**Appendix 2** (cont'd)

| Date | Air temp., °C | | | Wind speed, km/h | | | Wind direction* | | Barometric pressure, mb† | | Visibility,‡ km | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | 0700 | 1900 | 0700 | 1900 |
| 23 | 2 | 4 | 3.0 | 8.0 | 8.0 | 8.0 | SW | S | 06.7 | 06.0 | 8.0 | 16.0 |
| 24 | 1 | 2 | 1.5 | 16.0 | 8.0 | 12.0 | SE | SW | 04.8 | 04.2 | 0.4 | 0.4 |
| 25 | 3 | 3 | 3.0 | 4.8 | 4.8 | 4.8 | ENE | ESE | 04.2 | 02.6 | 40.0 | 8.0 |
| 26 | 2 | 3 | 2.5 | 3.2 | 9.6 | 6.4 | E | N | 01.9 | 03.8 | 0.4 | 3.2 |
| 27 | 2 | 2 | 2.0 | 1.6 | 8.0 | 4.8 | E | S | 05.7 | 10.5 | 1.6 | 0.2 |
| 28 | 4 | 4 | 4.0 | 6.4 | 19.2 | 12.8 | SW | S | 12.7 | 15.5 | 28.8 | 40.0 |
| 29 | 3 | 2 | 2.5 | 19.2 | 19.2 | 19.2 | S | S | 17.2 | 16.8 | 40.0 | 0.8 |
| 30 | 3 | 4 | 3.5 | 17.6 | 11.2 | 14.4 | SSW | S | 14.5 | 14.4 | 8.0 | 0.2 |
| 31 | 1 | 3 | 2.0 | 14.4 | 9.6 | 12.0 | W | NNW | 10.4 | 11.2 | 0.2 | 16.0 |
| 1 August | 1 | 2 | 1.5 | 19.2 | 4.8 | 12.0 | NW | SW | 11.8 | 14.0 | 32.0 | 40.0 |
| 2 | 1 | 1 | 1.0 | 22.1 | 22.4 | 22.25 | NW | WNW | 11.0 | 11.0 | 0.2 | 16.0 |
| 3 | −2 | −1 | −1.5 | 32.0 | 35.2 | 33.6 | NW | NW | 12.1 | 14.6 | 8.0 | 16.0 |
| 4 | −1 | 3 | 1.0 | 16.0 | 27.2 | 21.6 | NNW | N | 16.0 | 17.0 | 0.4 | 16.0 |
| 5 | 1 | 4 | 2.5 | 28.8 | 22.7 | 25.75 | N | N | 17.2 | 16.0 | 40.0 | 16.0 |
| 6 | 3 | 6 | 4.5 | 9.6 | 20.8 | 15.2 | NE | NNW | 15.0 | 09.2 | 32.0 | 40.0 |
| 7 | 4 | 2 | 3.0 | 38.4 | 17.6 | 28.0 | NNE | E | 06.2 | 06.2 | 0.4 | 1.6 |
| 8 | 1 | 2 | 1.5 | 30.4 | 28.8 | 29.6 | ENE | NE | 06.1 | 06.8 | 1.6 | 0.8 |
| 9 | 2 | 2 | 2.0 | 6.4 | 17.6 | 12.0 | E | N | 05.1 | 05.4 | 16.0 | 16.0 |
| 10 | 1 | 1 | 1.0 | 9.6 | 19.2 | 14.4 | S | E | 08.9 | 11.2 | 0.8 | 0.4 |
| 11 | −1 | 4 | 1.5 | 22.4 | 30.4 | 26.4 | E | ENE | 11.5 | 11.3 | 0.8 | 1.6 |
| 12 | 2 | 4 | 3.0 | 6.4 | 9.6 | 8.0 | E | E | 10.3 | 13.2 | 0.8 | 40.0 |
| 13 | 5 | 8 | 6.5 | 9.6 | 14.4 | 12.0 | SSE | SSE | 17.0 | 21.7 | 40.0 | 40.0 |
| 14 | 4 | 6 | 5.0 | 16.0 | 8.0 | 12.0 | SSW | WNW | 23.7 | 25.8 | 24.0 | 40.0 |
| 15 | 4 | 4 | 4.0 | 20.8 | 6.4 | 13.6 | WNW | WNW | 25.7 | 26.1 | 40.0 | 40.0 |
| 16 | 5 | 11 | 8.0 | 14.4 | 3.2 | 8.8 | NW | SSW | 24.7 | 21.5 | 40.0 | 40.0 |
| 17 | 9 | 13 | 11.0 | 6.4 | 11.2 | 8.8 | SSW | WNW | 18.7 | 13.4 | 40.0 | 40.0 |
| 18 | −1 | 2 | 0.5 | 25.6 | 32.0 | 28.8 | NNW | NNW | 13.2 | 15.0 | 0.8 | 24.0 |
| 19 | −1 | −1 | −1.0 | 33.6 | 36.8 | 35.2 | NNW | NNW | 15.3 | 17.2 | 0.8 | 8.0 |
| 20 | −2 | −1 | −1.5 | 38.4 | 35.2 | 36.8 | NW | WNW | 17.9 | 18.1 | 0.8 | 16.0 |
| 21 | −1 | −2 | −1.5 | 19.2 | 19.2 | 19.2 | NW | NW | 18.0 | 16.6 | 0.8 | 40.0 |
| 22 | −2 | −1 | −1.5 | 20.8 | 9.6 | 15.2 | NW | WNW | 13.1 | 10.8 | 40.0 | 40.0 |
| 23 | 0 | 0 | 0.0 | 3.2 | 9.6 | 6.4 | WNW | NE | 08.2 | 04.8 | 40.0 | 40.0 |
| 24 | −1 | −2 | −1.5 | 41.6 | 38.4 | 40.0 | NE | NNW | 98.0 | 00.7 | 0.2 | 24.0 |
| 25 | −4 | −3 | −3.5 | 41.6 | 6.4 | 24.0 | NW | NW | 00.8 | 00.8 | 24.0 | 1.6 |
| 26 | −6 | −5 | −5.5 | 24.0 | 28.8 | 26.4 | NW | NW | 01.0 | 01.9 | 24.0 | 1.6 |
| 27 | −4 | −1 | −2.5 | 8.0 | 27.2 | 17.6 | S | SW | 00.6 | 97.8 | 40.0 | 0.2 |
| 28 | 1 | 0 | 0.5 | 16.0 | 33.6 | 24.8 | W | WSW | 99.1 | 02.2 | 40.0 | 16.0 |
| 29 | −2 | −2 | −2.0 | 46.4 | 35.2 | 40.8 | WSW | NW | 04.9 | 06.8 | 0.4 | 0.8 |
| 30 | −2 | −1 | −1.5 | 6.4 | 9.6 | 8.0 | SW | SSW | 04.1 | 98.1 | 16.0 | 0.4 |
| 31 | −1 | −2 | −1.5 | 20.8 | 25.6 | 23.2 | NE | NW | 94.7 | 92.0 | 1.6 | 1.2 |
| 1 September | −6 | −5 | −5.5 | 32.0 | 35.2 | 33.6 | NW | ENE | 89.1 | 90.0 | 3.2 | 1.6 |
| 2 | −7 | −6 | −6.5 | 49.6 | 35.2 | 42.4 | ENE | NW | 90.9 | 03.1 | 0.2 | 0.2 |
| 3 | −7 | −7 | −7.0 | 19.2 | 16.0 | 17.6 | NW | NW | 08.0 | 11.2 | 24.0 | 24.0 |
| 4 | −7 | −6 | −6.5 | 17.6 | 12.8 | 15.2 | WNW | NW | 14.3 | 15.8 | 3.2 | 12.8 |
| 5 | −4 | −1 | −2.5 | 12.8 | 25.6 | 19.2 | W | S | 13.4 | 08.0 | 8.0 | 0.2 |
| 6 | −1 | −2 | −1.5 | 12.8 | 24.0 | 18.4 | S | NW | 06.9 | 99.2 | 0.2 | 0.8 |
| 7 | −8 | −6 | −7.0 | 19.2 | 27.2 | 23.2 | WNW | NW | 00.7 | 03.0 | 12.8 | 12.8 |
| 8 | −7 | −7 | −7.0 | 28.8 | 17.6 | 23.2 | NNW | NW | 05.7 | 08.6 | 4.8 | 16.0 |
| 9 | −7 | −7 | −7.0 | 12.8 | 22.4 | 17.6 | NNE | N | 07.2 | 05.6 | 0.4 | 16.0 |
| 10 | −5 | −6 | −5.5 | 20.8 | 33.6 | 27.2 | NW | NW | 04.2 | 06.1 | 16.0 | 1.6 |
| 11 | −7 | −6 | −6.5 | 24.0 | 24.0 | 24.0 | NW | NNW | 10.3 | 13.5 | 8.0 | 8.0 |
| 12 | −7 | −4 | −5.5 | 16.0 | 3.2 | 9.6 | NNW | W | 15.0 | 16.2 | 16.0 | 32.0 |
| 13 | −4 | −3 | −3.5 | 4.8 | 12.8 | 8.0 | W | W | 11.9 | 07.9 | 40.0 | 40.0 |
| 14 | −6 | −6 | −6.0 | 16.0 | 9.6 | 12.8 | W | SW | 03.5 | 01.7 | 4.8 | 0.4 |
| 15 | −6 | −8 | −7.0 | 24.0 | 28.8 | 26.4 | NNW | W | 99.5 | 5.6 | 0.4 | 16.0 |
| 16 | −9 | −8 | −8.5 | 17.6 | 27.2 | 22.4 | W | NNW | 09.5 | 9.6 | 40.0 | 8.0 |
| 17 | −10 | −9 | −9.5 | 27.2 | 22.4 | 24.8 | NW | NNW | 10.4 | 14.0 | 3.2 | 0.8 |
| 18 | −10 | −11 | −10.5 | 27.2 | 9.6 | 18.4 | NW | NNW | 16.2 | 17.2 | 0.4 | 0.2 |
| 19 | −9 | −7 | −8.0 | 6.4 | 12.8 | 9.6 | SW | S | 19.0 | 13.8 | 40.0 | 16.0 |
| 20 | −7 | −4 | −5.5 | 27.2 | 22.4 | 24.8 | S | S | 11.3 | 7.0 | 16.0 | 0.1 |
| 21 | −3 | −6 | −4.5 | 28.8 | 48.0 | 38.4 | NNW | NW | 03.0 | 8.0 | 0.1 | 0.1 |
| 22 | −11 | −7 | −9.0 | 6.4 | 24.0 | 15.2 | W | W | 09.0 | 7.1 | 24.0 | 8.0 |
| 23 | −10 | −12 | −11.0 | 12.8 | 24.0 | 18.4 | W | NW | 05.0 | 1.3 | 24.0 | 6.4 |
| 24 | −14 | — | −14.0 | 19.2 | — | 19.2 | NW | — | 03.1 | — | 24.0 | — |

**Appendix 2** (cont'd)

| Date | Air temp., °C | | | Wind speed, km/h | | | Wind direction* | | Barometric pressure, mb† | | Visibility,‡ km | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | 0700 | 1900 | 0700 | 1900 |
| 1976: | | | | | | | | | | | | |
| 6 May | −15 | −14 | −14.5 | 19.2 | 9.6 | 14.4 | WNW | W | — | — | 2.4 | 16.0 |
| 7 | −18 | −17 | −17.5 | 19.2 | 17.6 | 18.4 | NW | WNW | 01.0 | 00.4 | 12.8 | 16.0 |
| 8 | −19 | −19 | −19.0 | 4.8 | 25.6 | 15.2 | WNW | NNW | 99.1 | 01.8 | 8.0 | 4.8 |
| 9 | −19 | −19 | −19.0 | 24.0 | 27.2 | 25.6 | NNW | NW | 93.0 | 01.0 | 3.2 | 0.2 |
| 10 | −21 | −18 | −19.5 | 24.0 | 6.4 | 15.2 | NW | W | 05.2 | 03.4 | 11.2 | 24.0 |
| 11 | −17 | −16 | −16.5 | 12.8 | 24.0 | 18.4 | SW | N | 07.4 | 01.0 | 16.0 | 0.2 |
| 12 | −15 | −14 | −14.5 | 33.6 | 28.8 | 31.2 | N | NNW | 05.1 | 13.6 | 8.0 | 16.0 |
| 13 | −14 | −12 | −13.0 | 8.0 | 20.8 | 14.4 | NNW | NNE | 14.7 | 12.0 | 40.0 | 24.0 |
| 14 | −14 | −14 | −14.0 | 8.0 | 27.2 | 17.6 | NNW | WNW | 13.0 | 16.0 | 16.0 | 16.0 |
| 15 | −17 | −16 | −16.5 | 36.8 | 11.2 | 24.0 | W | SW | 26.0 | 25.0 | 0.2 | 40.0 |
| 16 | −15 | −14 | −14.5 | 12.8 | 22.4 | 17.6 | NW | NW | 22.0 | 17.3 | 16.0 | 40.0 |
| 17 | −18 | −17 | −17.5 | 40.0 | 27.2 | 33.6 | NW | NNW | 15.3 | 21.1 | 16.0 | 8.0 |
| 18 | −17 | −13 | −15.0 | 8.0 | 22.4 | 15.2 | NNW | N | 12.3 | 00.0 | 24.0 | 24.0 |
| 19 | −11 | −08 | −9.5 | 33.6 | 22.4 | 28.0 | NE | ENE | 05.0 | 03.3 | 0.4 | 0.2 |
| 20 | −12 | −11 | −11.5 | 51.2 | 8.0 | 29.6 | WNW | WSW | 12.9 | 26.5 | 0.2 | 32.0 |
| 21 | −12 | −12 | −12.0 | 24.0 | 36.8 | 30.2 | SSW | WSW | 22.0 | 22.0 | 0.2 | 0.2 |
| 22 | −16 | −12 | −14.0 | 24.0 | 19.2 | 21.6 | NW | SW | 30.8 | 30.5 | 24.0 | 32.0 |
| 23 | −12 | −11 | −11.5 | 4.8 | 8.0 | 6.4 | W | NW | 28.5 | 24.0 | 24.0 | 32.0 |
| 24 | −11 | −9 | −10.0 | 22.4 | 22.4 | 22.4 | WNW | NW | 18.0 | 02.4 | 40.0 | 40.0 |
| 25 | −11 | −9 | −10.0 | 41.6 | 44.8 | 43.2 | NW | NNW | 17.3 | 15.1 | 40.0 | 0.4 |
| 26 | −12 | −7 | −9.5 | 14.4 | 8.0 | 11.2 | NNW | S | 17.9 | 20.0 | 6.4 | 32.0 |
| 27 | −8 | −7 | −7.5 | 12.8 | 12.8 | 12.8 | E | N | 21.0 | 18.0 | 32.0 | 40.0 |
| 28 | −8 | −5 | −6.5 | 9.6 | 14.4 | 12.0 | E | NNE | 25.4 | 28.0 | 40.0 | 40.0 |
| 29 | −6 | 1 | −2.5 | 11.2 | 19.2 | 15.2 | NNE | NNE | 28.1 | 29.8 | 40.0 | 40.0 |
| 30 | 2 | 6 | 4.0 | 14.4 | 4.8 | 9.6 | NNE | NNW | 30.9 | 30.2 | 40.0 | 40.0 |
| 31 | −1 | −1 | −1.0 | 12.8 | 30.4 | 21.6 | NW | NNW | 29.5 | 26.9 | 40.0 | 40.0 |
| 1 June | −3 | −6 | −4.5 | 46.4 | 40.0 | 43.2 | W | NNW | 21.6 | 19.9 | 1.6 | 3.2 |
| 2 | −4 | −6 | −5.0 | 19.2 | 27.2 | 23.2 | NNW | WNW | 01.9 | 01.6 | 40.0 | 40.0 |
| 3 | −6 | −6 | −6.0 | 16.0 | 9.6 | 12.8 | NNW | N | 10.7 | 09.2 | 32.0 | 16.0 |
| 4 | −6 | −5 | −5.5 | 12.8 | 11.2 | 12.0 | N | N | 06.9 | 06.0 | 40.0 | 40.0 |
| 5 | −4 | −3 | −3.5 | 14.4 | 30.4 | 22.4 | N | NW | 01.8 | 99.8 | 24.0 | 0.2 |
| 6 | −4 | −3 | −3.5 | 3.2 | 11.2 | 7.2 | SE | E | 03.2 | 08.0 | 1.6 | 40.0 |
| 7 | −3 | −1 | −2.0 | 22.4 | 14.4 | 18.4 | W | NNW | 09.8 | 10.1 | 12.8 | 40.0 |
| 8 | −3 | 2 | −0.5 | 25.6 | 3.2 | 14.4 | WNW | NNW | 08.0 | 09.6 | 0.2 | 40.0 |
| 9 | 0 | 0 | 0 | 9.6 | 6.4 | 8.0 | NE | WSW | 01.1 | 01.3 | 40.0 | 24.0 |
| 10 | −6 | −4 | −5.0 | 14.4 | 38.4 | 26.4 | WNW | WNW | 11.3 | 12.0 | 0.2 | 0.2 |
| 11 | −3 | −2 | −2.5 | 36.8 | 36.8 | 36.8 | NW | NW | 09.2 | 06.0 | 16.0 | 0.2 |
| 12 | −3 | −2 | −2.5 | 30.4 | 30.4 | 30.4 | W | WNW | 04.1 | 05.5 | 0.2 | 9.6 |
| 13 | −2 | −3 | −2.5 | 19.2 | 27.2 | 23.2 | W | WNW | 07.7 | 09.5 | 16.0 | 0.2 |
| 14 | −3 | −2 | −2.5 | 28.8 | 6.4 | 17.6 | NNW | NW | 08.9 | 10.3 | 16.0 | 40.0 |
| 15 | −4 | −3 | −3.5 | 8.0 | 12.8 | 10.4 | S | S | 00.0 | 00.5 | 0.4 | 0.4 |
| 16 | −3 | −1 | −2.0 | 14.4 | 28.8 | 21.6 | SSE | SSE | 98.6 | 93.3 | 0.2 | 0.2 |
| 17 | −2 | −1 | −1.5 | 17.6 | 11.2 | 14.4 | WSW | SW | 92.5 | 00.5 | 3.2 | 0.4 |
| 18 | −1 | −1 | −1.0 | 8.0 | 8.0 | 8.0 | SSE | NNE | 90.9 | 04.3 | 0.4 | 32.0 |
| 19 | −2 | −1 | −1.5 | 6.4 | 22.4 | 14.4 | N | NNW | 06.8 | 09.5 | 16.0 | 16.0 |
| 20 | −1 | −1 | −1.0 | 1.6 | 16.0 | 8.8 | NNE | WNW | 10.6 | 12.7 | 40.0 | 9.6 |
| 21 | −2 | 1 | −0.5 | 25.6 | 11.2 | 18.4 | WNW | W | 12.5 | 14.8 | 0.2 | 40.0 |
| 22 | −2 | −1 | −1.5 | 4.8 | 19.2 | 12.0 | N | NNW | 01.7 | 01.6 | 4.8 | 40.0 |
| 23 | 0 | 2 | 1.0 | 17.6 | 17.6 | 17.6 | NNW | NW | 14.8 | 02.0 | 40.0 | 40.0 |
| 24 | 2 | 3 | 2.5 | 12.8 | 6.4 | 9.6 | NW | SSW | 16.8 | 15.3 | 40.0 | 40.0 |
| 25 | −1 | 0 | −0.5 | 9.6 | 20.8 | 15.2 | SE | NNW | 07.0 | 11.8 | 0.2 | 8.0 |
| 26 | −1 | 1 | 0.0 | 20.8 | 8.0 | 14.4 | WNW | W | 14.5 | 01.2 | 40.0 | 40.0 |
| 27 | 1 | 2 | 1.5 | 11.2 | 9.6 | 10.4 | WSW | SSW | 08.2 | 10.1 | 0.2 | 40.0 |
| 28 | −2 | −2 | −2.0 | 27.2 | 4.8 | 16.0 | WNW | S | 12.2 | 11.1 | 32.0 | 8.0 |
| 29 | −2 | −1 | −1.5 | 6.4 | 32.0 | 19.2 | ENE | WNW | 00.4 | 00.2 | 0.4 | 40.0 |
| 30 | −2 | −1 | −1.5 | 33.6 | 32.0 | 32.8 | W | WNW | 02.2 | 07.5 | 1.6 | 16.0 |

(cont'd next page)

**Appendix 2** (cont'd)

| Date | Air temp., °C | | | Wind speed, km/h | | | Wind direction* | | Barometric pressure, mb† | | Visibility,‡ km | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | 0700 | 1900 | 0700 | 1900 |
| 1 July | −1 | −1 | −1.0 | 14.4 | 12.8 | 13.6 | WNW | SSE | 12.7 | 09.5 | 16.0 | 16.0 |
| 2 | −1 | −1 | −1.0 | 48.0 | 27.2 | 37.6 | ESE | WNW | 10.1 | 99.7 | 0.0 | 0.0 |
| 3 | −2 | 0 | −1 | 41.6 | 17.6 | 29.6 | NW | NW | 00.0 | 01.6 | 32.0 | 32.0 |
| 4 | 0 | 3 | 1.5 | 8.0 | 0.0 | 4.0 | N | — | 14.1 | 09.4 | 40.0 | 40.0 |
| 5 | −1 | 1 | 0.0 | 8.0 | 4.8 | 6.4 | ENE | NE | 00.5 | 00.3 | 40.0 | 0.4 |
| 6 | 1 | 5 | 3.0 | 16.0 | 6.4 | 11.2 | NNE | NW | 04.9 | 05.9 | 40.0 | 40.0 |
| 7 | −1 | 2 | 0.5 | 1.6 | 24.0 | 12.8 | S | N | 06.6 | 08.8 | 0.4 | 40.0 |
| 8 | 2 | 1 | 1.5 | 22.6 | 33.6 | 28.1 | NNE | NNW | 00.6 | 11.1 | 40.0 | 11.2 |
| 9 | 0 | 1 | 0.5 | 12.4 | 17.6 | 15.0 | NE | NNW | 01.1 | 01.3 | 0.2 | 11.2 |
| 10 | −1 | 0 | −0.5 | 11.2 | 19.2 | 15.2 | NW | NW | 13.1 | 10.8 | 1.6 | 1.6 |
| 11 | 0 | 1 | 0.5 | 12.4 | 17.6 | 15.0 | WNW | NW | 00.9 | 00.7 | 0.8 | 0.8 |
| 12 | −1 | −1 | −1.0 | 38.4 | 40.0 | 39.2 | NW | WNW | 00.7 | 00.0 | 0.2 | 3.2 |
| 13 | −1 | −1 | −1.0 | 36.8 | 43.2 | 40.0 | WNW | WNW | 12.2 | 13.2 | 0.4 | 32.0 |
| 14 | 2 | 2 | 2.0 | 36.8 | 8.0 | 22.4 | WNW | WNW | 13.3 | 13.9 | 40.0 | 40.0 |
| 15 | 1 | 0 | 0.5 | 3.2 | 8.0 | 5.6 | SW | SE | 01.4 | 12.3 | 40.0 | 24.0 |
| 16 | 0 | 1 | 0.5 | 17.6 | 24.0 | 20.8 | NNW | WNW | 09.0 | 08.9 | 8.0 | 40.0 |
| 17 | 0 | 3 | 1.5 | 24.0 | 16.0 | 20.0 | NNW | SSE | 00.8 | 01.1 | 16.0 | 40.0 |
| 18 | 1 | 3 | 2.0 | 27.2 | 40.0 | 33.6 | NNW | NW | 10.9 | 10.9 | 40.0 | 40.0 |
| 19 | 1 | 3 | 2.0 | 44.8 | 49.6 | 47.2 | NW | NW | 07.3 | 04.1 | 40.0 | 40.0 |
| 20 | 3 | 7 | 5.0 | 33.6 | 12.8 | 23.2 | NNW | N | 04.2 | 07.0 | 40.0 | 40.0 |
| 21 | 6 | 8 | 7.0 | 4.8 | 14.4 | 9.6 | SW | NW | 01.2 | 01.3 | 40.0 | 40.0 |
| 22 | 5 | 8 | 6.5 | 22.4 | 19.2 | 20.8 | NW | WNW | 11.9 | 08.7 | 40.0 | 40.0 |
| 23 | 1 | 8 | 4.5 | 36.8 | 9.6 | 23.2 | ESE | SSE | 00.7 | 00.8 | 0.8 | 32.0 |
| 24 | 1 | 2 | 1.5 | 20.8 | 12.8 | 16.8 | NE | N | 01.0 | 12.0 | 0.2 | 0.8 |
| 25 | 1 | 9 | 5.0 | 12.8 | 20.8 | 16.8 | N | NNW | 14.0 | 01.7 | 0.4 | 40.0 |
| 26 | 6 | 11 | 8.5 | 17.6 | 12.8 | 15.2 | NNW | NNE | 01.8 | 02.2 | 40.0 | 40.0 |
| 27 | 6 | 9 | 7.5 | 12.8 | 8.0 | 10.4 | E | NNW | 23.0 | 21.1 | 40.0 | 40.0 |
| 28 | 9 | 11 | 10.0 | 28.8 | 17.6 | 23.2 | NW | NW | 19.6 | 20.3 | 40.0 | 40.0 |
| 29 | 3 | 2 | 2.5 | 27.2 | 28.8 | 28.0 | NE | NE | 23.9 | 27.2 | 32.0 | 32.0 |
| 30 | −1 | 9 | 4.0 | 20.8 | 16.0 | 18.4 | NE | WNW | 25.8 | 20.3 | 0.2 | 40.0 |
| 31 | 9 | 6 | 7.5 | 6.4 | 30.4 | 18.4 | SW | E | 13.0 | 06.0 | 40.0 | 0.2 |
| 1 August | 0 | 1 | 0.5 | 36.8 | 35.2 | 36.0 | WNW | NW | 05.0 | 01.9 | 0.4 | 24.0 |
| 2 | 0 | 4 | 2.0 | 35.2 | 32.0 | 33.6 | NW | NNE | 96.7 | 98.5 | 1.2 | 40.0 |
| 3 | 2 | 2 | 2.0 | 35.2 | 51.2 | 43.2 | NW | WNW | 99.8 | 99.9 | 16.0 | 0.8 |
| 4 | 0 | 1 | 0.5 | 44.8 | 40.0 | 42.8 | NW | WNW | 02.1 | 94.1 | 24.0 | 16.0 |
| 5 | 0 | 0 | 0.0 | 14.4 | 32.0 | 23.2 | WNW | WNW | 95.8 | 99.0 | 0.8 | 0.4 |
| 6 | 0 | 2 | 1.0 | 20.8 | 22.4 | 21.6 | NW | NW | 96.0 | 04.0 | 0.4 | 40.0 |
| 7 | 1 | −1 | 0.0 | 17.6 | 14.4 | 16.0 | WNW | SSW | 99.4 | 94.6 | 6.4 | 0.2 |
| 8 | −2 | −1 | −1.5 | 20.8 | 4.8 | 12.8 | NW | SW | 93.4 | 97.0 | 32.0 | 40.0 |
| 9 | 0 | 1 | 0.5 | 24.0 | 27.2 | 25.6 | WNW | WNW | 01.5 | 05.3 | 0.4 | 16.0 |
| 10 | −1 | −1 | −1.0 | 22.4 | 24.0 | 23.2 | NW | NW | 09.7 | 13.5 | 0.2 | 0.4 |
| 11 | −2 | 0 | −1.0 | 24.0 | 48.0 | 36.0 | NW | WNW | 13.2 | 13.7 | 0.4 | 32.0 |
| 12 | 2 | 1 | 1.5 | 20.8 | 27.2 | 24.0 | WNW | WNW | 11.9 | 99.1 | 40.0 | 0.2 |
| 13 | −2 | −1 | −1.5 | 24.0 | 41.6 | 32.8 | NNW | NNW | 10.0 | 09.0 | 8.0 | 9.6 |
| 14 | −1 | −1 | −1.0 | 33.6 | 38.4 | 36.0 | NW | WNW | 08.9 | 11.0 | 1.6 | 0.8 |
| 15 | −2 | −1 | −1.5 | 41.6 | 30.4 | 36.0 | WNW | W | 14.7 | 16.9 | 0.8 | 0.4 |
| 16 | −1 | −1 | −1.0 | 24.0 | 27.2 | 25.6 | NNW | NW | 16.6 | 15.4 | 1.6 | 9.6 |
| 17 | 2 | 3 | 2.5 | 6.4 | 6.4 | 6.4 | NW | WSW | 16.7 | 16.0 | 40.0 | 40.0 |
| 18 | 4 | 3 | 3.5 | 25.6 | 16.0 | 20.8 | ESE | E | 15.1 | 10.2 | 40.0 | 40.0 |
| 19 | 2 | 1 | 1.5 | 16.0 | 6.4 | 11.2 | E | S | 30.0 | 98.0 | 40.0 | 0.2 |
| 20 | 0 | −2 | −1.0 | 9.6 | 35.2 | 22.4 | W | WNW | 96.0 | 99.4 | 0.2 | 3.2 |
| 21 | −3 | −1 | −2.0 | 30.4 | 35.2 | 32.8 | WNW | WNW | 02.5 | 02.2 | 16.0 | 16.0 |
| 22 | −4 | −2 | −3.0 | 8.0 | 8.0 | 8.0 | SSW | S | 99.1 | 92.4 | 0.4 | 0.4 |
| 23 | −2 | −4 | −3.0 | 25.6 | 33.6 | 29.6 | WNW | W | 93.0 | 00.1 | 0.8 | 16.0 |
| 24 | −4 | −3 | −3.5 | 16.0 | 27.2 | 21.6 | S | WNW | 95.0 | 92.3 | 0.2 | 0.4 |
| 25 | −3 | −2 | −2.5 | 41.6 | 46.4 | 44.0 | WNW | N | 94.9 | 97.0 | 0.4 | 24.0 |
| 26 | −4 | −3 | −3.5 | 35.2 | 35.2 | 35.2 | NW | NW | 04.7 | 07.2 | 40.0 | 40.0 |
| 27 | −3 | — | −3.0 | 32.0 | 33.6 | 32.8 | N | WNW | 08.3 | 11.2 | 40.0 | 40.0 |
| 28 | −3 | −1 | −2.0 | 35.2 | 3.2 | 19.2 | WNW | NW | 11.5 | 16.4 | 40.0 | 40.0 |
| 29 | −3 | −2 | −2.5 | 9.6 | 9.6 | 9.6 | NW | NW | 18.9 | 17.0 | 40.0 | 40.0 |
| 30 | −1 | −1 | −1.0 | 46.4 | 54.4 | 50.4 | NW | NNW | 14.0 | 19.2 | 40.0 | 40.0 |
| 31 | −1 | −2 | −1.5 | 20.8 | 24.0 | 22.4 | N | NE | 24.0 | 23.0 | 40.0 | 0.2 |

**Appendix 2** (cont'd)

| | Air temp., °C | | | Wind speed, km/h | | | Wind direction* | | Barometric pressure, mb† | | Visibility,‡ km | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | 0700 | 1900 | 0700 | 1900 |
| 1 September | −3 | −2 | −2.5 | 16.0 | 8.0 | 12.0 | ENE | NW | 17.3 | 14.0 | 0.2 | 40.0 |
| 2 | −1 | −1 | −1.0 | 11.2 | 19.2 | 15.2 | W | WNW | 11.6 | 11.9 | 40.0 | 0.4 |
| 3 | −3 | −2 | −2.5 | 19.2 | 32.0 | 25.6 | WNW | NW | 11.1 | 10.0 | 0.4 | 8.0 |
| 4 | −3 | −1 | −2.0 | 12.8 | 12.8 | 12.8 | NW | N | 10.2 | 13.0 | 1.6 | 40.0 |
| 5 | −1 | −3 | −2.0 | 3.2 | 17.6 | 10.4 | WNW | NE | 15.3 | 17.0 | 40.0 | 0.2 |
| 6 | −3 | −2 | −2.5 | 17.6 | 6.4 | 12.0 | NE | E | 10.0 | 23.0 | 0.2 | 40.0 |
| 7 | −2 | −3 | −2.5 | 11.2 | 22.4 | 16.8 | E | E | 25.2 | 25.3 | 0.2 | 32.0 |
| 8 | −3 | −3 | −3.0 | 24.0 | 32.0 | 28.0 | NE | NE | 23.9 | 13.7 | 0.2 | 12.8 |
| 9 | −2 | −2 | −2.0 | 62.4 | 51.2 | 56.8 | NE | NE | 96.6 | 93.0 | 12.8 | 0.2 |
| 10 | −1 | −2 | −1.5 | 36.8 | 24.0 | 30.4 | NNE | N | 95.0 | 98.0 | 0.2 | 32.0 |
| 11 | −3 | −2 | −2.5 | 14.4 | 24.0 | 19.2 | N | NNW | 90.0 | 03.0 | 40.0 | 40.0 |
| 12 | −3 | −3 | −3.0 | 12.8 | 12.8 | 12.8 | NNW | NW | 09.0 | 10.2 | 40.0 | 40.0 |
| 13 | −4 | −4 | −4.0 | 24.0 | 11.2 | 17.6 | NW | NW | 11.4 | 13.3 | 32.0 | 32.0 |
| 14 | −4 | −5 | −4.5 | 22.4 | 28.8 | 25.6 | NNW | NW | 15.0 | 12.1 | 40.0 | 40.0 |
| 15 | −3 | −4 | −3.5 | 24.0 | 17.6 | 20.8 | NNW | NNW | 11.0 | 10.0 | 40.0 | 40.0 |
| 16 | −4 | −7 | −5.5 | 14.4 | 11.2 | 12.8 | NNE | NNE | 08.8 | 00.0 | 40.0 | 8.0 |
| 17 | −6 | −7 | −6.5 | 17.6 | 25.6 | 21.6 | NW | NW | 10.0 | 10.0 | 40.0 | 0.4 |
| 18 | −8 | −8 | −8.0 | 19.2 | 19.2 | 19.2 | NNW | WNW | 11.7 | 12.1 | 32.0 | 32.2 |
| 19 | −8 | −8 | −8.0 | 16.0 | 41.6 | 28.8 | W | W | 10.0 | 10.0 | 0.4 | 24.0 |
| 20 | −7 | −8 | −7.5 | 36.8 | 41.6 | 39.2 | NW | NW | 12.3 | 15.0 | 24.0 | 32.0 |
| 21 | −8 | −7 | −7.5 | 32.0 | 30.4 | 31.2 | N | NNE | 18.0 | 21.1 | 32.0 | 32.0 |
| 22 | −8 | −6 | −7.0 | 6.4 | 12.8 | 9.6 | NNE | NNW | 20.4 | 17.9 | 32.0 | 40.0 |
| 23 | −5 | −4 | −4.5 | 30.4 | 19.2 | 24.8 | NNW | NNW | 14.0 | 13.1 | 40.0 | 8.0 |
| 24 | −4 | −4 | −4.0 | 4.8 | 9.6 | 7.2 | ESE | N | 12.0 | 20.0 | 0.8 | 0.2 |
| 25 | −4 | −3 | −3.5 | 27.2 | 8.0 | 17.6 | N | NE | 19.0 | 13.2 | 16.0 | 4.8 |
| 26 | −3 | −4 | −3.5 | 19.2 | 19.2 | 19.2 | NNW | NNE | 01.0 | 12.0 | 8.0 | 0.4 |
| 27 | −3 | — | −3.0 | 24.0 | — | 24.0 | NNE | — | 11.4 | — | 0.0 | — |
| 1977: | | | | | | | | | | | | |
| 2 June | — | −1 | −1.0 | — | 6.4 | 6.4 | — | NNW | — | 15.9 | — | 40.0 |
| 3 | −4 | −3 | −3.5 | 22.4 | 25.6 | 24.0 | NNE | NNE | 18.4 | 18.2 | 16.0 | 16.0 |
| 4 | −3 | −2 | −2.5 | 17.6 | 36.8 | 27.2 | NW | NW | 17.8 | 14.3 | 24.0 | 40.0 |
| 5 | −4 | −2 | −3.0 | 20.8 | 17.6 | 19.2 | WNW | E | 15.7 | 19.9 | 3.2 | 40.0 |
| 6 | −2 | −1 | −1.5 | 20.8 | 8.0 | 14.4 | NNE | NNE | 19.4 | 21.0 | 16.0 | 24.0 |
| 7 | −2 | −1 | −1.5 | 4.8 | 1.6 | 3.2 | NNE | NNE | 22.8 | 24.2 | 4.8 | 0.4 |
| 8 | −3 | 1 | −1.0 | 4.8 | 9.6 | 7.2 | NE | NNE | 24.8 | 23.5 | 0.4 | 40.0 |
| 9 | −2 | 1 | −0.5 | 17.6 | 22.4 | 20.0 | NNE | NNE | 20.8 | 17.5 | 40.0 | 40.0 |
| 10 | −2 | 0 | −1.0 | 28.8 | 32.0 | 30.4 | NNE | N | 11.0 | 07.3 | 0.4 | 1.6 |
| 11 | −1 | 2 | 0.5 | 32.0 | 27.2 | 29.5 | NNE | NNE | 06.1 | 07.8 | 32.0 | 40.0 |
| 12 | 0 | 3 | 1.5 | 36.8 | 25.6 | 31.2 | N | NE | 06.9 | 08.5 | 40.0 | 40.0 |
| 13 | 0 | 3 | 1.5 | 30.4 | 14.4 | 22.4 | N | NE | 10.3 | 12.6 | 0.4 | 40.0 |
| 14 | 3 | 0 | 1.5 | 33.6 | 30.4 | 32.0 | NE | N | 12.2 | 13.5 | 40.0 | 40.0 |
| 15 | −1 | −2 | −1.5 | 24.0 | 4.8 | 14.4 | NNE | NNE | 13.0 | 11.9 | 0.2 | 1.6 |
| 16 | 3 | 3 | 3.0 | 3.2 | 6.4 | 4.8 | NE | NE | 11.1 | 10.5 | 3.2 | 8.0 |
| 17 | 0 | 1 | 0.5 | 12.8 | 27.2 | 20.0 | N | NW | 12.4 | 16.9 | 32.0 | 40.0 |
| 18 | 0 | 2 | 1.0 | 9.6 | 4.8 | 7.2 | W | SSW | 19.8 | 22.0 | 0.2 | 40.0 |
| 19 | 0 | 5 | 2.5 | 6.4 | 12.8 | 9.6 | SSW | WSW | 21.9 | 20.2 | 40.0 | 40.0 |
| 20 | −2 | −1 | −1.5 | 14.4 | 16.0 | 15.2 | SSW | SSW | 16.8 | 12.0 | 0.4 | 0.4 |
| 21 | 3 | 1 | 2.0 | 14.4 | 27.2 | 20.8 | W | NW | 07.6 | 08.9 | 40.0 | 0.2 |
| 22 | 1 | 4 | 2.5 | 19.2 | 22.4 | 20.8 | N | N | 11.1 | 12.5 | 40.0 | 40.0 |
| 23 | 3 | 1 | 2.0 | 20.8 | 38.4 | 29.6 | NW | WNW | 10.3 | 06.4 | 40.0 | 24.0 |
| 24 | 1 | 7 | 4.0 | 25.6 | 8.0 | 16.8 | NNW | NNW | 07.1 | 07.2 | 40.0 | 40.0 |
| 25 | 2 | 0 | 1.0 | 14.4 | 32.0 | 23.2 | NE | NNE | 04.6 | 04.9 | 40.0 | 40.0 |
| 26 | 0 | 1 | 0.5 | 14.4 | 30.4 | 22.4 | NE | NNE | 08.0 | 09.5 | 40.0 | 32.0 |
| 27 | — | −2 | −1.0 | 32.0 | 32.0 | 32.0 | N | E | 06.9 | 06.4 | 1.6 | 0.4 |
| 28 | −2 | 0 | −1.0 | 30.4 | 51.2 | 40.8 | NE | ENE | 10.8 | 09.4 | 0.2 | 16.0 |
| 29 | −1 | −1 | −1.0 | 25.6 | 16.0 | 20.8 | E | E | 09.7 | 09.9 | 0.4 | 0.4 |
| 30 | −1 | −1 | −1.0 | 19.2 | 28.8 | 24.0 | NE | NE | 10.2 | 13.2 | 0.2 | 0.2 |

(cont'd next page)

**Appendix 2** (cont'd)

| Date | Air temp., °C | | | Wind speed, km/h | | | Wind direction* | | Barometric pressure, mb† | | Visibility,‡ km | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | 0700 | 1900 | 0700 | 1900 |
| 1 July | −1 | 3 | 1.0 | 19.2 | 9.6 | 14.4 | NE | ENE | 15.4 | 16.3 | 0.2 | 40.0 |
| 2 | 0 | −1 | −0.5 | 30.4 | 48.0 | 39.2 | NE | NE | 16.1 | 13.1 | 0.4 | 0.4 |
| 3 | −1 | 0 | −0.5 | 32.0 | 27.2 | 29.6 | NE | NNE | 13.1 | 14.8 | 0.4 | 16.0 |
| 4 | −1 | 3 | 1.0 | 25.6 | 33.6 | 29.6 | NE | NE | 15.8 | 17.4 | 16.0 | 16.0 |
| 5 | 1 | 8 | 4.5 | 17.6 | 9.6 | 13.6 | NE | NW | 18.0 | 19.0 | 16.0 | 40.0 |
| 6 | 5 | 6 | 5.5 | 16.0 | 32.0 | 24.0 | NW | W | 18.4 | 18.2 | 40.0 | 40.0 |
| 7 | 4 | 5 | 4.5 | 8.0 | 24.0 | 16.0 | WNW | NW | 17.7 | 17.1 | 40.0 | 40.0 |
| 8 | 5 | 8 | 6.5 | 14.4 | 9.6 | 12.0 | NW | W | 13.8 | 11.9 | 40.0 | 40.0 |
| 9 | 5 | 6 | 5.5 | 9.6 | 17.6 | 13.6 | NW | NW | 11.6 | 11.8 | 40.0 | 40.0 |
| 10 | 1 | 1 | 1.0 | 35.2 | 25.6 | 30.4 | E | NNE | 12.3 | 16.0 | 32.0 | 8.0 |
| 11 | 1 | 4 | 2.5 | 41.6 | 41.6 | 41.6 | NE | NNE | 18.4 | 21.3 | 16.0 | 40.0 |
| 12 | 4 | 7 | 5.5 | 22.4 | 9.6 | 16.0 | NNE | NE | 21.4 | 19.1 | 40.0 | 40.0 |
| 13 | 5 | 8 | 6.5 | 22.4 | 20.8 | 21.6 | NNE | NE | 15.6 | 14.5 | 40.0 | 40.0 |
| 14 | 4 | 1 | 2.5 | 28.8 | 36.8 | 32.8 | NNE | NE | 14.2 | 14.8 | 40.0 | 16.0 |
| 15 | 1 | 1 | 1.0 | 38.4 | 16.0 | 27.2 | NNE | NNE | 11.7 | 09.8 | 0.4 | 0.2 |
| 16 | 6 | 2 | 4.0 | 14.4 | 30.4 | 22.4 | NNE | NNE | 08.7 | 07.5 | 40.0 | 24.0 |
| 17 | 2 | 1 | 1.5 | 32.0 | 27.2 | 29.6 | NE | ENE | 07.8 | 06.9 | 0.2 | 0.2 |
| 18 | 1 | 6 | 3.5 | 17.6 | 6.4 | 12.0 | NE | NE | 01.0 | 11.8 | 16.0 | 40.0 |
| 19 | 4 | 1 | 2.5 | 11.2 | 14.4 | 12.8 | NE | NE | 12.9 | 12.5 | 40.0 | 40.0 |
| 20 | 7 | 13 | 10.0 | 9.6 | 20.8 | 15.2 | NNE | WNW | 10.4 | 09.2 | 40.0 | 40.0 |
| 21 | 8 | 10 | 9.0 | 27.2 | 30.4 | 28.8 | WNW | W | 09.4 | 10.7 | 40.0 | 40.0 |
| 22 | 7 | 9 | 8.0 | 33.6 | 40.0 | 36.8 | NNW | NNW | 12.0 | 10.7 | 40.0 | 40.0 |
| 23 | 3 | 4 | 3.5 | 38.4 | 44.8 | 41.6 | NW | NW | 08.8 | 11.4 | 32.0 | 40.0 |
| 24 | 2 | 9 | 5.5 | 25.6 | 27.2 | 26.4 | NW | NW | 14.4 | 15.7 | 40.0 | 40.0 |
| 25 | 6 | 9 | 7.5 | 22.4 | 24.0 | 23.2 | NW | NNW | 13.5 | 12.2 | 40.0 | 40.0 |
| 26 | 5 | 2 | 3.5 | 33.6 | 30.4 | 32.0 | WNW | WNW | 10.1 | 10.6 | 40.0 | 16.0 |
| 27 | 1 | 1 | 1.0 | 27.2 | 36.8 | 32.0 | NW | WNW | 09.7 | 06.4 | 0.4 | 0.8 |
| 28 | −1 | 1 | 0.0 | 36.8 | 24.0 | 30.4 | WNW | WNW | 01.8 | 98.0 | 0.4 | 8.0 |
| 29 | 1 | 2 | 1.5 | 28.8 | 25.6 | 27.2 | NNW | NE | 97.7 | 01.3 | 32.0 | 0.2 |
| 30 | 4 | 5 | 4.5 | 27.2 | 35.2 | 31.2 | NNW | NW | 03.9 | 05.3 | 40.0 | 40.0 |
| 31 | 0 | 2 | 1.0 | 35.2 | 12.8 | 24.0 | NNE | NNE | 04.9 | 07.6 | 0.4 | 8.0 |
| 1 August | 1 | 6 | 3.5 | 4.8 | 6.4 | 5.6 | NNE | NNE | 11.4 | 14.9 | 40.0 | 40.0 |
| 2 | 1 | 1 | 1.0 | 27.2 | 40.0 | 33.6 | NE | NE | 15.0 | 14.6 | 0.2 | 0.2 |
| 3 | 1 | 4 | 2.5 | 32.0 | 41.6 | 36.8 | NE | NE | 16.0 | 15.0 | 0.4 | 0.4 |
| 4 | 4 | 3 | 3.5 | 27.2 | 20.8 | 24.0 | NE | ENE | 14.9 | 17.9 | 0.4 | 16.0 |
| 5 | 5 | 7 | 6.0 | 36.8 | 19.2 | 28.0 | E | ENE | 15.2 | 17.8 | 40.0 | 40.0 |
| 6 | 6 | 8 | 7.0 | 17.6 | 4.8 | 11.2 | NE | NE | 17.7 | 18.4 | 40.0 | 40.0 |
| 7 | 7 | 10 | 8.5 | 3.2 | 17.6 | 10.4 | NNW | NW | 18.2 | 18.0 | 40.0 | 40.0 |
| 8 | 6 | 4 | 5.0 | 0.0 | 8.0 | 4.0 | — | WNW | 16.5 | 14.5 | 40.0 | 40.0 |
| 9 | 2 | 3 | 2.5 | 1.6 | 4.8 | 3.2 | SW | E | 13.2 | 13.8 | 0.4 | 0.4 |
| 10 | 2 | 2 | 2.0 | 24.0 | 27.2 | 25.6 | NE | E | 13.1 | 14.3 | 40.0 | 32.0 |
| 11 | 1 | 2 | 1.5 | 28.8 | 33.6 | 31.2 | E | E | 15.8 | 18.9 | 0.2 | 40.0 |
| 12 | 2 | 2 | 2.0 | 14.4 | 28.8 | 21.6 | NE | WNW | 20.2 | 15.9 | 40.0 | 40.0 |
| 13 | 0 | 1 | 0.5 | 19.2 | 1.6 | 10.4 | NW | NE | 12.8 | 14.1 | 1.6 | 0.8 |
| 14 | 1 | 2 | 1.5 | 24.0 | 30.4 | 27.2 | NE | NE | 15.1 | 14.5 | 8.0 | 40.0 |
| 15 | 1 | 2 | 1.5 | 17.6 | 28.8 | 23.2 | — | NNE | 13.3 | 14.3 | 32.0 | 0.4 |
| 16 | 1 | 3 | 2.0 | 0.0 | 11.2 | 5.6 | — | NNE | 16.4 | 16.4 | 32.0 | 40.0 |
| 17 | 2 | 2 | 2.0 | 0.0 | 1.6 | 0.8 | — | SSE | 14.4 | 12.6 | 40.0 | 24.0 |
| 18 | −1 | 0 | −0.5 | 0.0 | 20.8 | 10.4 | — | NNE | 11.3 | 11.1 | 0.4 | 32.0 |
| 19 | 1 | 1 | 1.0 | 54.4 | 40.0 | 47.2 | NNE | ENE | 06.4 | 08.4 | 0.4 | 0.2 |
| 20 | 1 | 2 | 1.5 | 16.0 | 16.0 | 16.0 | ENE | NNE | 15.1 | 20.1 | 24.0 | 1.2 |
| 21 | 1 | 3 | 2.0 | 33.6 | 32.0 | 32.8 | NNE | NE | 21.1 | 22.6 | 16.0 | 32.0 |
| 22 | 6 | 10 | 8.0 | 20.8 | 0.0 | 10.4 | NE | — | 20.1 | 24.1 | 40.0 | 40.0 |
| 23 | 4 | 6 | 5.0 | 0.0 | 19.2 | 9.6 | — | WNW | 24.2 | 23.1 | 40.0 | 40.0 |
| 24 | 0 | 4 | 2.0 | 20.8 | 14.4 | 17.6 | NNE | NNE | 21.2 | 20.6 | 40.0 | 40.0 |
| 25 | 1 | 1 | 1.0 | 20.8 | 30.4 | 25.6 | NE | E | 19.2 | 17.4 | 32.0 | 40.0 |
| 26 | 0 | 2 | 1.0 | 27.2 | 12.8 | 20.0 | NE | NE | 14.8 | 12.1 | 32.0 | 32.0 |
| 27 | 2 | 4 | 3.0 | 4.8 | 11.2 | 8.0 | NNE | NNW | 09.7 | 06.4 | 40.0 | 40.0 |
| 28 | 1 | 2 | 1.5 | 19.2 | 20.8 | 20.0 | NNW | WNW | 05.9 | 05.8 | 40.0 | 40.0 |
| 29 | 0 | 1 | 0.5 | 0.0 | 25.6 | 12.8 | — | NW | 06.4 | 08.8 | 32.0 | 16.0 |
| 30 | −2 | −1 | −1.5 | 17.6 | 28.8 | 23.2 | NNW | WNW | 10.5 | 13.2 | 0.8 | 0.4 |
| 31 | −2 | −1 | −1.5 | 32.0 | 14.4 | 23.2 | WNW | WNW | 14.3 | 15.0 | 3.2 | 8.0 |

**Appendix 2** (cont'd)

| Date | Air temp., °C |  |  | Wind speed, km/h |  |  | Wind direction* |  | Barometric pressure, mb† |  | Visibility,‡ km |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | $\bar{x}$ | 0700 | 1900 | 0700 | 1900 | 0700 | 1900 |
| 1 September | −2 | 2 | 0.0 | 4.8 | 6.4 | 5.6 | SW | WNW | 13.4 | 11.9 | 8.0 | 32.0 |
| 2 | 1 | −1 | 0.0 | 6.4 | 28.8 | 17.6 | W | W | 09.9 | 09.4 | 32.0 | 40.0 |
| 3 | −4 | 1 | −1.5 | 24.0 | 22.4 | 23.2 | WNW | SW | 09.0 | 01.9 | 1.6 | 1.6 |
| 4 | −2 | −3 | −2.5 | 22.4 | 44.8 | 33.6 | W | W | 00.5 | 02.2 | 32.0 | 0.4 |
| 5 | −3 | −3 | −3.0 | 22.4 | 30.4 | 26.4 | W | W | 00.9 | 02.9 | 0.8 | 40.0 |
| 6 | −6 | −5 | −5.5 | 22.4 | 27.2 | 24.8 | NW | NW | 06.7 | 10.3 | 10.0 | 40.0 |
| 7 | −4 | −3 | −3.5 | 19.2 | 25.6 | 22.4 | — | NW | 11.4 | 11.3 | 24.0 | 3.2 |
| 8 | −4 | −5 | −4.5 | 9.6 | 11.2 | 10.4 | NW | WNW | 08.9 | 09.9 | 8.0 | 40.0 |
| 9 | −4 | −2 | −3.0 | 6.4 | 27.2 | 16.8 | NNW | NW | 07.0 | 07.0 | 40.0 | 32.0 |
| 10 | −2 | −6 | −4.0 | 8.0 | 28.8 | 18.4 | WSW | NW | 04.1 | 04.9 | 0.4 | 40.0 |
| 11 | −8 | −4 | −6.0 | 8.0 | 27.2 | 17.6 | NW | W | 03.5 | 96.4 | 40.0 | 1.6 |
| 12 | −8 | −7 | −7.5 | 30.4 | 17.6 | 24.0 | WNW | W | 98.4 | 00.8 | 24.0 | 0.8 |
| 13 | −10 | −7 | −8.5 | 28.8 | 51.2 | 40.0 | WNW | WNW | 05.2 | 05.5 | 24.0 | 0.1 |
| 14 | −9 | −8 | −8.5 | 30.4 | 14.4 | 22.4 | WNW | W | 13.2 | 18.2 | 8.0 | 16.0 |
| 15 | −8 | −9 | −8.5 | 17.6 | 16.0 | 16.8 | NNW | NW | 29.0 | 28.8 | 40.0 | 40.0 |
| 16 | −8 | −9 | −8.5 | 12.8 | 3.2 | 8.0 | WNW | WNW | 28.1 | 25.9 | 24.0 | 40.0 |
| 17 | −7 | −4 | −5.5 | 14.4 | 22.4 | 18.4 | W | WSW | 20.8 | 14.0 | 40.0 | 40.0 |
| 18 | −2 | −3 | −2.5 | 4.8 | 28.8 | 16.8 | SSW | SSE | 09.4 | 04.3 | 0.4 | 32.0 |
| 19 | −3 | −4 | −3.5 | 14.4 | 44.8 | 29.6 | WSW | SW | 02.5 | 00.6 | 40.0 | 1.6 |
| 20 | −4 | — | −4.0 | 28.8 | — | 28.8 | SW | — | 14.3 | — | 0.8 | — |

* Note that wind direction is the direction from which the wind is blowing and is measured in tens of degrees: N = 36, NNE = 02, NE = 04, ENE = 07, E = 09, ESE = 11, SE = 14, SSE = 16, S = 18, SSW = 20, SW = 22, WSW = 25, W = 27, WNW = 29, NW = 32, NNW = 34.

† Barometric pressure was taken with an aneroid barometer and reduced to sea level in millibars and tenths with the initial 9 or 10 omitted (e.g., 997.5 is entered as 97.5, or 1013.2 = 13.2).

‡ Horizontal visibility at eye level is the farthest distance (maximum to known fixed point = 40 km) that can be seen for half or more of the horizon.

**Appendix 3**
Daily counts of individual Thick-billed Murres on 12 study plots along the East Cliff colony between 1700 and 1900 h (CDT), 1975–77*†

| | Study plot | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | G1 | G4 | M | N | Q1 | Q3 | Q4 | S1 | S2 | S3 | S4 | U |
| 1975: | | | | | | | | | | | | |
| 3 June | 3 | 0 | — | — | — | — | — | — | — | — | — | — |
| 4 | 53 | 63 | — | — | — | — | — | — | — | — | — | — |
| 5 | 67 | 83 | — | — | — | — | — | — | — | — | — | — |
| 6 | 49 | 67 | — | — | — | — | — | — | — | — | — | — |
| 7 | 6 | 4 | — | — | — | — | — | — | — | — | — | — |
| 8 | 18 | 15 | — | — | — | — | — | — | — | — | — | — |
| 9 | 35 | 27 | — | — | — | — | — | — | — | — | — | — |
| 10 | 19 | 11 | — | — | — | — | — | — | — | — | — | — |
| 11 | 57 | 73 | — | — | — | — | — | — | — | — | — | — |
| 12 | 64 | 88 | — | — | — | — | — | — | — | — | — | — |
| 13 | 39 | 34 | — | — | — | — | — | — | — | — | — | — |
| 14 | 59 | 62 | — | — | — | — | — | — | — | — | — | — |
| 15 | 53 | 95 | — | — | — | — | — | — | — | — | — | — |
| 16 | 58 | 74 | — | — | — | — | — | — | — | — | — | — |
| 17 | 47 | 45 | — | — | — | — | — | — | — | — | — | — |
| 18 | 52 | 59 | — | — | — | — | — | — | — | — | — | — |
| 19 | 33 | 42 | — | — | — | — | — | — | — | — | — | — |
| 20 | 82 | 89 | — | — | — | — | — | — | — | — | — | — |
| 21 | 12 | 11 | — | — | — | — | — | — | — | — | — | — |
| 22 | 53 | 57 | — | — | — | — | — | — | — | — | — | — |
| 23 | 72 | 94 | — | — | — | — | — | — | — | — | — | — |
| 24 | 70 | — | — | — | — | — | — | — | — | — | — | — |
| 25 | 51 | — | — | — | — | — | — | — | — | — | — | — |
| 26 | 61 | 70 | — | — | — | — | — | — | — | — | — | — |
| 27 | 62 | 58 | — | — | — | — | — | — | — | — | — | — |
| 28 | 72 | 87 | — | — | — | — | — | — | — | — | — | — |
| 29 | 58 | 68 | — | — | — | — | — | — | — | — | — | — |
| 30 | 61 | 74 | — | — | — | — | — | — | — | — | — | — |
| 1 July | 77 | 85 | — | — | — | — | — | — | — | — | — | — |
| 2 | 75 | 79 | — | — | — | — | — | — | — | — | — | — |
| 3 | 71 | 74 | — | — | — | — | — | — | — | — | — | — |
| 4 | 73 | 81 | — | — | — | — | — | — | — | — | — | — |
| 5 | 57 | — | — | — | — | — | — | — | — | — | — | — |
| 6 | 67 | 90 | — | — | — | — | — | — | — | — | — | — |
| 7 | 76 | 79 | — | — | — | — | — | — | — | — | — | — |
| 8 | 66 | 83 | — | — | — | — | — | — | — | — | — | — |
| 9 | 77 | 82 | — | — | — | — | — | — | — | — | — | — |
| 10 | — | — | — | — | — | — | — | — | — | — | — | — |
| 11 | 76 | 90 | — | — | — | — | — | — | — | — | — | — |
| 12 | 67 | 74 | — | — | — | — | — | — | — | — | — | — |
| 13 | 71 | 84 | — | — | — | — | — | — | — | — | — | — |
| 14 | 73 | 81 | — | — | — | — | — | — | — | — | — | — |
| 15 | 74 | 95 | — | — | — | — | — | — | — | — | — | — |
| 16 | 76 | 85 | — | — | — | — | — | — | — | — | — | — |
| 17 | 58 | 67 | — | — | — | — | — | — | — | — | — | — |
| 18 | 85 | 94 | — | — | — | — | — | — | — | — | — | — |
| 19 | 71 | 89 | — | — | — | — | — | — | — | — | — | — |
| 20 | 88 | 104 | — | — | — | — | — | — | — | — | — | — |
| 21 | 70 | — | — | — | — | — | — | — | — | — | — | — |
| 22 | 67 | 75 | — | — | — | — | — | — | — | — | — | — |
| 23 | 87 | 98 | — | — | — | — | — | — | — | — | — | — |
| 24 | 72 | 73 | — | — | — | — | — | — | — | — | — | — |
| 25 | 85 | 86 | — | — | — | — | — | — | — | — | — | — |
| 26 | 76 | 82 | — | — | — | — | — | — | — | — | — | — |
| 27 | 74 | — | — | — | — | — | — | — | — | — | — | — |
| 28 | 84 | 88 | — | — | — | — | — | — | — | — | — | — |
| 29 | 75 | 80 | — | — | — | — | — | — | — | — | — | — |
| 30 | 81 | 89 | — | — | — | — | — | — | — | — | — | — |
| 31 | 77 | 94 | — | — | — | — | — | — | — | — | — | — |

**Appendix 3** (cont'd)

| | Study plot | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | G1 | G4 | M | N | Q1 | Q3 | Q4 | S1 | S2 | S3 | S4 | U |
| 1 August | 86 | 86 | — | — | — | — | — | — | — | — | — | — |
| 2 | — | — | — | — | — | — | — | — | — | — | — | — |
| 3 | 77 | 92 | — | — | — | — | — | — | — | — | — | — |
| 4 | 77 | 90 | — | — | — | — | — | — | — | — | — | — |
| 5 | 74 | 97 | — | — | — | — | — | — | — | — | — | — |
| 6 | 78 | 90 | — | — | — | — | — | — | — | — | — | — |
| 7 | 74 | 86 | — | — | — | — | — | — | — | — | — | — |
| 8 | 83 | 91 | — | — | — | — | — | — | — | — | — | — |
| 9 | 67 | 83 | — | — | — | — | — | — | — | — | — | — |
| 10 | 77 | 85 | — | — | — | — | — | — | — | — | — | — |
| 11 | — | — | — | — | — | — | — | — | — | — | — | — |
| 12 | — | — | — | — | — | — | — | — | — | — | — | — |
| 13 | 86 | 94 | — | — | — | — | — | — | — | — | — | — |
| 14 | 78 | 92 | — | — | — | — | — | — | — | — | — | — |
| 15 | 81 | 88 | — | — | — | — | — | — | — | — | — | — |
| 16 | 79 | 93 | — | — | — | — | — | — | — | — | — | — |
| 17 | 78 | 83 | — | — | — | — | — | — | — | — | — | — |
| 18 | 73 | 77 | — | — | — | — | — | — | — | — | — | — |
| 19 | 77 | 75 | — | — | — | — | — | — | — | — | — | — |
| 20 | 84 | 81 | — | — | — | — | — | — | — | — | — | — |
| 21 | 62 | 72 | — | — | — | — | — | — | — | — | — | — |
| 22 | 75 | 76 | — | — | — | — | — | — | — | — | — | — |
| 23 | 55 | 59 | — | — | — | — | — | — | — | — | — | — |
| 24 | 49 | 57 | — | — | — | — | — | — | — | — | — | — |
| 25 | 42 | 38 | — | — | — | — | — | — | — | — | — | — |
| 26 | 26 | 34 | — | — | — | — | — | — | — | — | — | — |
| 27 | 10 | 12 | — | — | — | — | — | — | — | — | — | — |
| 28 | 10 | 13 | — | — | — | — | — | — | — | — | — | — |
| 29 | 8 | 7 | — | — | — | — | — | — | — | — | — | — |
| 1976: | | | | | | | | | | | | |
| 7 May | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12 | 0 | 1 | 1 | 0 | 0 | 4 | 0 | 10 | 10 | 0 | 0 | 0 |
| 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 15 | 0 | 0 | 0 | 0 | 0 | 11 | 1 | 4 | 4 | 1 | 17 | 0 |
| 16 | 4 | 4 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 20 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 21 | 0 | 0 | 0 | 0 | 0 | 9 | 4 | 7 | 1 | 40 | 17 | 0 |
| 22 | 6 | 13 | 12 | 0 | 0 | 43 | 18 | 85 | 55 | 11 | 51 | 0 |
| 23 | 14 | 25 | 23 | 40 | 8 | 1 | 8 | 52 | 28 | 1 | 17 | 0 |
| 24 | 17 | 36 | 12 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 25 | 0 | 0 | 0 | 0 | 0 | 35 | 41 | 105 | 60 | 17 | 41 | 12 |
| 26 | 26 | 34 | 45 | 50 | 8 | 46 | 30 | 72 | 36 | 14 | 69 | 0 |
| 27 | 3 | 13 | 32 | 57 | 0 | 7 | 10 | 44 | 26 | 7 | 13 | 8 |
| 28 | 12 | 5 | 24 | 19 | 1 | 5 | 7 | 2 | 11 | 3 | 0 | 4 |
| 29 | 16 | 5 | 20 | 5 | 0 | 51 | 15 | 122 | 70 | 11 | 22 | 19 |
| 30 | 23 | 36 | 42 | 40 | 7 | 6 | 0 | 50 | 23 | 0 | 0 | 4 |
| 31 | 6 | 0 | 21 | 7 | 1 | | | | | | | |

(cont'd next page)

**Appendix 3** (cont'd)

| | Study plot | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Date** | **G1** | **G4** | **M** | **N** | **Q1** | **Q3** | **Q4** | **S1** | **S2** | **S3** | **S4** | **U** |
| 1 June | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2 | 13 | 19 | 22 | 10 | 5 | 4 | 2 | 24 | 19 | 7 | 36 | 5 |
| 3 | 60 | 78 | 80 | 115 | 100 | 98 | 112 | 240 | 115 | 50 | 113 | 55 |
| 4 | 43 | 77 | 41 | 117 | 91 | 116 | 82 | 227 | 106 | 32 | 87 | 75 |
| 5 | 13 | 1 | 3 | 0 | 1 | 5 | 0 | 0 | 0 | 2 | 0 | 1 |
| 6 | 45 | 40 | 50 | 68 | 42 | 40 | 31 | 56 | 22 | 24 | 36 | 37 |
| 7 | 86 | 90 | 87 | 120 | 97 | 110 | 94 | 220 | 118 | 46 | 113 | 98 |
| 8 | 21 | 36 | 47 | 52 | 39 | 49 | 23 | 52 | 31 | 19 | 22 | 12 |
| 9 | 57 | 64 | 66 | 67 | 63 | 62 | 52 | 135 | 61 | 16 | 51 | 35 |
| 10 | 27 | 22 | 32 | 54 | 56 | 31 | 50 | 28 | 41 | 20 | 34 | 31 |
| 11 | 29 | 22 | 31 | 45 | 18 | 41 | 42 | 34 | 16 | 17 | 53 | 20 |
| 12 | 64 | 76 | 66 | 114 | 107 | 104 | 101 | 126 | 77 | 52 | 114 | 68 |
| 13 | 102 | 113 | 100 | 157 | 167 | 141 | 124 | 345 | 166 | 85 | 127 | 110 |
| 14 | 81 | 65 | 67 | 92 | 106 | 77 | 94 | 196 | 81 | 34 | 82 | 75 |
| 15 | 67 | 57 | 60 | 68 | 103 | 91 | 84 | 120 | 78 | 34 | 100 | 60 |
| 16 | 8 | 12 | 23 | 10 | 18 | 15 | 14 | (12)† | 16 | (5) | 12 | 10 |
| 17 | 50 | 56 | 46 | 77 | 91 | 76 | 78 | 121 | 61 | 37 | 70 | 47 |
| 18 | 96 | 89 | 87 | 149 | 158 | 107 | 127 | 249 | 139 | 60 | 117 | 112 |
| 19 | 78 | 85 | 68 | 129 | 145 | 108 | 110 | 119 | 107 | 55 | 101 | 81 |
| 20 | 52 | 65 | 48 | 67 | 96 | 72 | 84 | 166 | 89 | 33 | 63 | 63 |
| 21 | 55 | 63 | 43 | 89 | 103 | 90 | 83 | 139 | 66 | 24 | 71 | 64 |
| 22 | 78 | 75 | 61 | 99 | 117 | 96 | 94 | 197 | 91 | 40 | 84 | 83 |
| 23 | 70 | 73 | 70 | 98 | 102 | 93 | 85 | 178 | 89 | 38 | 90 | 74 |
| 24 | 66 | 69 | 61 | 99 | 106 | 77 | 96 | 175 | 79 | 47 | 94 | 67 |
| 25 | 53 | 55 | 42 | 46 | 72 | 85 | 78 | 142 | 72 | 37 | 84 | 43 |
| 26 | 73 | 86 | 67 | 112 | 108 | 98 | 97 | 189 | 90 | 43 | 86 | 61 |
| 27 | 64 | 72 | 56 | 104 | 111 | 93 | 97 | 164 | 78 | 42 | 80 | 58 |
| 28 | 78 | 87 | 71 | 125 | 147 | 115 | 101 | 220 | 81 | 52 | 107 | 78 |
| 29 | 66 | 78 | 64 | 121 | 133 | 94 | 98 | 193 | 89 | 52 | 89 | 78 |
| 30 | 66 | 69 | 63 | 119 | 115 | 95 | 94 | 162 | 94 | 49 | 115 | 77 |
| 1 July | 79 | 87 | 70 | 134 | 173 | 109 | 104 | 219 | 94 | 54 | 106 | 78 |
| 2 | (77) | (91) | (73) | (132) | (165) | (107) | (104) | (222) | (97) | (54) | (105) | (82) |
| 3 | 74 | 95 | 76 | 130 | 157 | 104 | 105 | 224 | 101 | 54 | 104 | 85 |
| 4 | 81 | 92 | 76 | 133 | 169 | 101 | 104 | 237 | 99 | 44 | 97 | 87 |
| 5 | 55 | 67 | 69 | 121 | 123 | 107 | 97 | 172 | 85 | 45 | 107 | 71 |
| 6 | 83 | 91 | 68 | 136 | 140 | 100 | 90 | 206 | 87 | 41 | 87 | 79 |
| 7 | 69 | 90 | 65 | 129 | 122 | 107 | 111 | 202 | 87 | 49 | 106 | 82 |
| 8 | 65 | 82 | 56 | 108 | 131 | 98 | 97 | 168 | 76 | 47 | 106 | 69 |
| 9 | 63 | 74 | 64 | 122 | 128 | 107 | 100 | 204 | 92 | 53 | 108 | 74 |
| 10 | 75 | 78 | 67 | 114 | 125 | 99 | 97 | 196 | 87 | 44 | 96 | 74 |
| 11 | 66 | 75 | 69 | 131 | 147 | 105 | 101 | 208 | 88 | (44) | (97) | 85 |
| 12 | 57 | 65 | 55 | 109 | (119) | 97 | 88 | 187 | 78 | 44 | 90 | 72 |
| 13 | 67 | 81 | 71 | 128 | 100 | 111 | 103 | 206 | 90 | 50 | 95 | 75 |
| 14 | 70 | 92 | 76 | 123 | 104 | 106 | 96 | 226 | 87 | 49 | 95 | 74 |
| 15 | 71 | 86 | 69 | 117 | 133 | 106 | 99 | 202 | 93 | (53) | (102) | 76 |
| 16 | 74 | 78 | 68 | 121 | 135 | 104 | 99 | 212 | 92 | 52 | 100 | 80 |
| 17 | 75 | 86 | 74 | 130 | 143 | 106 | 100 | 208 | 92 | 51 | 97 | 78 |
| 18 | 70 | 80 | 74 | 124 | 145 | 105 | 110 | 186 | 88 | 51 | 106 | 81 |
| 19 | 70 | 83 | 58 | 138 | 145 | 108 | 102 | 213 | 103 | (55) | (105) | 72 |
| 20 | 88 | 90 | 83 | 144 | 160 | 109 | 101 | 230 | 102 | 55 | 105 | 87 |
| 21 | 70 | 81 | 77 | 128 | 137 | 105 | 109 | 203 | 89 | 51 | 109 | 74 |
| 22 | 69 | 77 | 59 | 121 | 140 | 100 | 92 | 210 | 84 | 50 | 99 | 72 |
| 23 | 68 | 85 | 69 | 111 | 130 | 100 | 99 | 191 | 87 | 52 | 114 | 67 |
| 24 | 79 | 80 | 78 | 126 | 158 | 116 | 104 | 233 | 84 | 49 | 110 | 79 |
| 25 | 79 | 88 | 65 | 131 | 126 | 103 | 105 | 216 | 84 | 53 | 98 | 72 |
| 26 | 79 | 90 | 77 | 136 | 150 | 110 | 108 | 222 | 95 | 54 | 101 | 75 |
| 27 | 70 | 94 | 75 | 124 | 153 | 109 | 107 | 215 | 96 | 56 | 101 | 85 |
| 28 | 69 | 84 | 67 | 134 | 126 | 106 | 97 | 212 | 82 | 47 | 93 | 69 |
| 29 | (80) | (98) | 78 | 140 | 180 | 114 | 112 | 231 | 94 | 60 | 110 | 87 |
| 30 | 70 | 92 | 73 | 129 | 144 | 108 | 107 | 237 | 98 | 57 | 97 | 78 |
| 31 | 65 | 83 | 77 | 124 | 144 | 92 | 102 | 219 | 86 | 52 | 96 | 73 |

**Appendix 3** (cont'd)

| Date | Study plot | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | G1 | G4 | M | N | Q1 | Q3 | Q4 | S1 | S2 | S3 | S4 | U |
| 1 August | 85 | 106 | 81 | 184 | 178 | 124 | 113 | 245 | 102 | 58 | 110 | 86 |
| 2 | 79 | 85 | 74 | 147 | 147 | 118 | 110 | 216 | 95 | 60 | 115 | 88 |
| 3 | 70 | 94 | 84 | 146 | 160 | 107 | 107 | 212 | 98 | 52 | 105 | 86 |
| 4 | 78 | 103 | 92 | 158 | 162 | 111 | 106 | 237 | 101 | 52 | 105 | 87 |
| 5 | 73 | 89 | 88 | 143 | (148) | (101) | (97) | 209 | 95 | 53 | 94 | 81 |
| 6 | 75 | 101 | 79 | 156 | 172 | 117 | 102 | 225 | 90 | 57 | 110 | (86) |
| 7 | 75 | (70) | 67 | 128 | (149) | (106) | 94 | 243 | 92 | 53 | 106 | 85 |
| 8 | 85 | 95 | 87 | 167 | 174 | 124 | 114 | 238 | 113 | 67 | 126 | 101 |
| 9 | 74 | 100 | 77 | 160 | 166 | 120 | 113 | 236 | 94 | 46 | 91 | 85 |
| 10 | 74 | 86 | 78 | 148 | (162) | (117) | (110) | 239 | 91 | (45) | (89) | 90 |
| 11 | 69 | 90 | (69) | (157) | (156) | (118) | (107) | 234 | 95 | (62) | (115) | (91) |
| 12 | 69 | 78 | 69 | 157 | 156 | 118 | 107 | 238 | 93 | 62 | 115 | 91 |
| 13 | 86 | 97 | 77 | 158 | 187 | 122 | 110 | 244 | 95 | 56 | 105 | 94 |
| 14 | 73 | 85 | 82 | 155 | 141 | 105 | 97 | 201 | 87 | 56 | 99 | 92 |
| 15 | 75 | 89 | (80) | (156) | (157) | (113) | (105) | (223) | (91) | (54) | (100) | (92) |
| 16 | 76 | 93 | 78 | 158 | 179 | 122 | 116 | 245 | 95 | 53 | 101 | 92 |
| 17 | 74 | 84 | 73 | 140 | 144 | 112 | 98 | 222 | 92 | 54 | 99 | 77 |
| 18 | 67 | 82 | 72 | 137 | 164 | 107 | 94 | 224 | 85 | 55 | 109 | 77 |
| 19 | 62 | 73 | 69 | 143 | 147 | 115 | 85 | 213 | 93 | 52 | 89 | 87 |
| 20 | 51 | 69 | 60 | 126 | 156 | 120 | 103 | 195 | 78 | 48 | 95 | 88 |
| 21 | 63 | 72 | 78 | 135 | 157 | 110 | 83 | 209 | 86 | 44 | 88 | 79 |
| 22 | 13 | 28 | 23 | 48 | 62 | 36 | 33 | 108 | 33 | 27 | 39 | 36 |
| 23 | 38 | 54 | 55 | 110 | 13 | 63 | 38 | 145 | 59 | 26 | 44 | 53 |
| 24 | 29 | 40 | 37 | 82 | 34 | 68 | 24 | 140 | 47 | 26 | 54 | 37 |
| 25 | (18) | (25) | (37) | (68) | (29) | (45) | (18) | (117) | (40) | (16) | (31) | (35) |
| 26 | 8 | 10 | 38 | 54 | 24 | 22 | 13 | 94 | 33 | 6 | 8 | 34 |
| 27 | 4 | 3 | 23 | 43 | 12 | 15 | 4 | 86 | 19 | 3 | 7 | 26 |
| 28 | 3 | 0 | 6 | 13 | 8 | 6 | 3 | 55 | 12 | 3 | 1 | 6 |
| 29 | 3 | 0 | 11 | 18 | 7 | 5 | 2 | 57 | 10 | 4 | 4 | 7 |
| 30 | 3 | 0 | 5 | 13 | 6 | 3 | 1 | 39 | 5 | 2 | 1 | 6 |
| 31 | 3 | — | — | — | — | — | — | — | — | — | — | — |
| 1 September | 2 | 0 | 1 | 13 | 7 | 0 | 1 | 17 | 1 | (4) | (6) | 4 |
| 2 | — | — | — | — | — | — | — | — | — | — | — | — |
| 3 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 3 | 1 | 1 | 0 | 2 |
| 4 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 1 |
| 5 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 0 | 0 |
| 6 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 7 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

(cont'd next page)

**Appendix 3** (cont'd)

| Date | G1 | G4 | M | N | Q1 | Q3 | Q4 | S1 | S2 | S3 | S4 | U |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1977: | | | | | | | | | | | | |
| 2 June | 50 | 59 | 53 | 95 | 62 | 102 | 54 | 170 | 104 | 39 | 99 | 65 |
| 3 | 21 | 20 | 22 | 22 | 3 | 62 | 13 | 24 | 30 | 3 | 14 | 3 |
| 4 | 22 | 18 | 10 | 6 | 8 | 24 | 2 | 41 | 29 | 1 | 1 | 1 |
| 5 | 28 | 26 | — | — | — | — | — | — | — | — | — | — |
| 6 | 38 | 42 | 16 | 52 | 61 | 37 | 28 | 56 | 37 | 15 | 50 | 8 |
| 7 | 56 | 61 | 43 | 104 | 93 | 81 | 63 | 189 | 106 | 31 | 86 | — |
| 8 | 43 | 40 | — | — | — | — | — | — | — | — | — | — |
| 9 | 15 | 27 | 8 | 4 | 16 | 12 | 8 | 5 | 0 | 11 | 4 | 1 |
| 10 | 7 | 1 | 6 | 0 | 1 | 6 | 4 | 0 | 0 | 0 | 0 | 0 |
| 11 | 42 | 43 | 27 | 27 | 18 | 35 | 9 | 26 | 19 | 8 | 14 | 1 |
| 12 | 44 | 34 | 13 | 17 | 20 | 50 | 23 | 64 | 53 | 8 | 16 | 1 |
| 13 | 56 | 58 | 37 | 68 | 50 | 58 | 49 | 167 | 84 | 7 | 53 | 28 |
| 14 | 18 | 69 | 55 | 84 | 65 | 40 | 70 | 92 | 52 | 23 | 34 | 24 |
| 15 | 51 | 34 | 30 | 25 | 39 | 35 | 38 | 59 | 29 | 22 | 36 | 27 |
| 16 | 45 | 50 | 47 | 96 | 109 | 81 | 87 | 144 | 73 | 46 | 82 | 79 |
| 17 | 45 | 69 | 56 | 77 | 87 | 92 | 80 | 148 | 82 | 21 | 41 | 39 |
| 18 | 41 | 59 | 43 | 64 | 71 | 47 | 54 | 116 | 56 | 23 | 45 | 27 |
| 19 | 37 | 53 | — | — | — | — | — | — | — | — | — | — |
| 20 | 11 | — | — | 38 | — | — | — | 37 | 19 | — | — | 17 |
| 21 | 34 | 44 | 34 | 78 | — | — | — | 112 | 63 | 36 | 71 | 39 |
| 22 | 84 | 96 | 75 | 162 | 157 | 102 | 117 | 228 | 103 | 54 | 100 | 95 |
| 23 | 43 | 65 | 53 | 104 | 96 | 69 | 75 | 185 | 72 | 22 | 54 | 56 |
| 24 | 54 | 79 | 56 | 111 | 93 | 67 | 73 | 168 | 72 | 28 | 58 | 46 |
| 25 | 50 | 58 | 65 | 100 | 110 | 83 | 91 | 145 | 66 | 41 | 68 | 66 |
| 26 | 44 | 55 | 37 | 102 | 109 | 75 | 93 | 141 | 74 | 36 | 85 | 74 |
| 27 | 12 | 18 | — | — | — | — | — | 47 | 30 | — | — | 11 |
| 28 | 40 | 53 | 62 | 108 | 127 | 88 | 88 | 174 | 76 | 34 | 83 | 64 |
| 29 | 75 | 99 | 61 | 148 | — | — | — | 227 | 105 | — | — | 83 |
| 30 | 64 | 70 | — | — | — | — | — | 173 | 68 | — | — | 57 |
| 1 July | 75 | 99 | 74 | 160 | 162 | 97 | 107 | 233 | 104 | 47 | 94 | 83 |
| 2 | 35 | 49 | — | — | — | — | — | 146 | 60 | — | — | 57 |
| 3 | 58 | 76 | 65 | 110 | — | — | — | 171 | 68 | — | — | 59 |
| 4 | 72 | 83 | 66 | 154 | 161 | 118 | 119 | 212 | 92 | 53 | 110 | 81 |
| 5 | 90 | 105 | 72 | 160 | 169 | 112 | 102 | 253 | 103 | 55 | 115 | 84 |
| 6 | 62 | 90 | 62 | 142 | 141 | 100 | 113 | 206 | 85 | 46 | 101 | 71 |
| 7 | 74 | 94 | 65 | 146 | 137 | 86 | 110 | 215 | 87 | 51 | 96 | 75 |
| 8 | 75 | 100 | 66 | 135 | 153 | 99 | 90 | 220 | 96 | 46 | 97 | 76 |
| 9 | 56 | 93 | 58 | 139 | 153 | 99 | 113 | 221 | 92 | 49 | 91 | 71 |
| 10 | 61 | 73 | 57 | 133 | 153 | 97 | 113 | 199 | 78 | 50 | 100 | 71 |
| 11 | 79 | 86 | 76 | 148 | 163 | 109 | 111 | 223 | 93 | 49 | 102 | 84 |
| 12 | 88 | 97 | 77 | 155 | 158 | 110 | 124 | 238 | 97 | 50 | 114 | 85 |
| 13 | 68 | 73 | 62 | 138 | 151 | 115 | 103 | 219 | 82 | 51 | 106 | 71 |
| 14 | 57 | 76 | 64 | 123 | 151 | 91 | 105 | 203 | 81 | 46 | 101 | 69 |
| 15 | 84 | 102 | 65 | 150 | — | — | — | 246 | 98 | 51 | 111 | 83 |
| 16 | 65 | 76 | 58 | 125 | — | — | — | 217 | 81 | 44 | 101 | 67 |
| 17 | 53 | — | — | — | — | — | — | 194 | 76 | — | — | 54 |
| 18 | 90 | 97 | 76 | 165 | 186 | 121 | 114 | 259 | 96 | 65 | 125 | 89 |
| 19 | 83 | 88 | 70 | 140 | 174 | 115 | 123 | 228 | 86 | 55 | 103 | 92 |
| 20 | 88 | 111 | 81 | 153 | 160 | 106 | 112 | 249 | 100 | 54 | 109 | 86 |
| 21 | 83 | 80 | 69 | 146 | 156 | 87 | 99 | 229 | 86 | 52 | 93 | 81 |
| 22 | 83 | 88 | 66 | 169 | 140 | 112 | 104 | 225 | 86 | 49 | 98 | 83 |
| 23 | 71 | 97 | 77 | 166 | 169 | 117 | 101 | 240 | 85 | 56 | 101 | 87 |
| 24 | 98 | 107 | 87 | 157 | 160 | 112 | 108 | 273 | 100 | 54 | 94 | 85 |
| 25 | 86 | 108 | 87 | 169 | 180 | 116 | 116 | 250 | 96 | 61 | 105 | 85 |
| 26 | 83 | 100 | 83 | 185 | 195 | 113 | 121 | 263 | 93 | 65 | 123 | 92 |
| 27 | 80 | 92 | 83 | 154 | — | — | — | 261 | 105 | 63 | 115 | 94 |
| 28 | 81 | 93 | 74 | 185 | 193 | 125 | 132 | 239 | 87 | 57 | 111 | 80 |
| 29 | 75 | 95 | 78 | 160 | 197 | 134 | 124 | 262 | 99 | 64 | 129 | 88 |
| 30 | 97 | 145 | 93 | 185 | 183 | 104 | 112 | 275 | 105 | 57 | 102 | 96 |
| 31 | 104 | 111 | 83 | 164 | 209 | 136 | 124 | 289 | 110 | 70 | 124 | 96 |

**Appendix 3** (cont'd)

| Date | Study plot | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | G1 | G4 | M | N | Q1 | Q3 | Q4 | S1 | S2 | S3 | S4 | U |
| 1 August | 89 | 104 | 94 | 175 | 208 | 117 | 133 | 288 | 105 | 65 | 128 | 91 |
| 2 | 56 | — | — | — | — | — | — | — | — | — | — | 72 |
| 3 | 74 | 86 | — | — | — | 115 | 115 | 245 | 100 | — | — | 92 |
| 4 | 83 | 107 | 81 | 162 | 203 | 108 | 119 | 260 | 118 | 66 | 109 | 99 |
| 5 | 81 | 110 | 86 | 173 | 223 | 131 | 130 | 279 | 100 | 67 | 118 | 97 |
| 6 | 98 | 106 | 74 | 170 | 202 | 113 | 113 | 251 | 100 | 56 | 110 | 99 |
| 7 | 86 | 109 | 82 | 158 | 165 | 112 | 111 | 253 | 101 | 57 | 103 | 86 |
| 8 | 93 | 119 | 89 | 173 | 190 | 116 | 121 | 270 | 106 | 67 | 124 | 91 |
| 9 | 94 | 104 | 81 | 165 | 182 | 112 | 109 | 269 | 102 | 62 | 109 | 91 |
| 10 | 73 | 111 | 77 | 170 | 213 | 120 | 119 | 236 | 103 | 62 | 106 | 86 |
| 11 | 80 | 106 | 74 | 161 | 197 | 122 | 133 | 250 | 99 | 66 | 113 | 91 |
| 12 | 82 | 104 | 78 | 186 | 176 | 113 | 119 | 251 | 99 | 59 | 106 | 85 |
| 13 | 98 | 121 | 83 | 172 | 203 | 130 | 127 | 260 | 94 | 67 | 124 | 93 |
| 14 | 73 | 89 | 74 | 155 | 193 | 118 | 121 | 244 | 90 | 55 | 116 | 83 |
| 15 | 60 | 81 | 66 | 150 | 166 | 103 | 103 | 219 | 82 | 57 | 106 | 90 |
| 16 | 72 | 96 | 88 | 170 | 194 | 113 | 113 | 254 | 103 | 57 | 109 | 99 |
| 17 | 78 | 87 | 83 | 154 | 179 | 113 | 107 | 221 | 98 | 53 | 105 | 85 |
| 18 | 74 | 86 | 69 | 143 | — | — | — | 217 | 76 | 50 | 97 | 84 |
| 19 | 39 | 32 | — | — | — | — | — | 138 | 47 | — | — | 62 |
| 20 | 81 | 98 | 80 | 153 | 180 | 116 | 110 | 244 | 102 | 58 | 95 | 90 |
| 21 | 71 | 80 | 65 | 145 | 169 | 100 | 107 | 215 | 72 | 50 | 91 | 86 |
| 22 | 79 | 84 | 55 | 124 | 147 | 90 | 89 | 208 | 75 | 52 | 87 | 75 |
| 23 | 62 | 76 | 59 | 150 | 148 | 107 | 93 | 225 | 73 | 48 | 92 | 82 |
| 24 | 71 | 78 | 69 | 126 | 150 | 81 | 87 | 202 | 72 | 43 | 84 | 75 |
| 25 | 59 | 74 | 65 | 142 | 156 | 92 | 100 | 231 | 71 | 49 | 98 | 80 |
| 26 | 61 | 76 | 49 | 120 | 129 | 85 | 75 | 183 | 66 | 39 | 64 | 74 |
| 27 | 46 | 60 | 47 | 92 | 113 | 65 | 70 | 165 | 57 | 38 | 64 | 59 |
| 28 | 54 | 74 | 67 | 111 | 113 | 73 | 73 | 168 | 61 | 43 | 53 | 57 |
| 29 | 39 | 43 | 38 | 81 | 80 | 52 | 53 | 140 | 52 | 29 | 55 | 42 |
| 30 | 28 | 36 | 27 | 65 | 58 | 24 | 22 | 87 | 23 | 22 | 27 | 30 |
| 31 | — | — | — | — | — | — | — | — | — | — | — | — |
| 1 September | 13 | 19 | 17 | 37 | 12 | 3 | 5 | 50 | 18 | 11 | 6 | 16 |
| 2 | 5 | 4 | 5 | 12 | 5 | 0 | 2 | 24 | 5 | 5 | 3 | 10 |
| 3 | 5 | 3 | 6 | 5 | 3 | 0 | 1 | 12 | 3 | 3 | 3 | 7 |
| 4 | 4 | 3 | 5 | 4 | 3 | 0 | 1 | 9 | 3 | 3 | 3 | 6 |
| 5 | 4 | 3 | 5 | 4 | 3 | 0 | 1 | 9 | 3 | 3 | 2 | 6 |
| 6 | 2 | 1 | 4 | 1 | 0 | 0 | 1 | 6 | 1 | 1 | 1 | 5 |
| 7 | 2 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 4 |
| 8 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| 9 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

* Dash indicates no data.

† Figures in parentheses are interpolated.

## Appendix 4
## Instructions for making behaviour watches on study plots G3 and S1

Procedure no. — Details of instructions*

*General instructions:*

1. Set up the spotting scope on the site so that the field includes about 200 birds.
2. Take a minute to study the field. Decide which birds it will be possible to observe accurately and count only these. Ignore any behaviour involving other birds. Do not attempt to watch more than 250 birds.
3. Record the number of birds at the start and finish of the observation period, the number of copulations, the number of attempted copulations, the number of fights, and the number of birds arriving and departing.
4. Score all observations by a single stroke.
5. If copulation or attempted copulation occurs within 20 s of the arrival of one of the birds, and the sex is noted, score ♂ or ♀ instead of stroke.
6. Attempted copulation is an instance where the ♀ makes no attempt to bend forward, but instead tries to stand up, twisting its neck around.
7. If a fight occurs as a result of an arrival or an attempted copulation, score both events.
8. If a departure occurs following a fight score + instead of stroke in the departure column (not recorded in 1976).
9. Only score a fight once if the birds involved are known to be the same, but score all copulations.
10. A fight is scored when both participants in an interaction peck one another several times. Do not score interactions where one bird flees immediately.
11. Score all arrivals and departures even if the bird is known to be the same one.

*Additional instructions for watches at S1:*

1. Count the number of birds on the area of S1 outlined on the photographs.
2. Begin watch on the hour and finish after 60 minutes.
3. Record the following:
   - a. *Arrivals* — If there is no greeting ceremony or copulation record a single stroke. If there is a copulation or an attempted copulation record +. If there is a greeting ceremony (pair give "arrr" call with their necks arched, sitting bird stands up), then record the time and the egg number, thus — 1705/16.
   - b. *Departures* — Record with a single stroke. If departure follows a fight use +. If egg is left unattended record the time. For birds leaving after an incubation change, record the time and the egg number as for arrivals. Departures of prospectors recorded only in 1975.
   - c. *Copulations* — As above under General instructions.
   - d. *Exchanges* — Record time and egg number for birds changing incubation duty.
   - e. *Food deliveries* — If food is brought to a chick, record as for an arrival, but underline the number. If a fish can be seen put F after the number.

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* In 1977 notes were made using cassette tape-recorders and transcribed later. In 1976 and 1977 times of incubation changes and departures were recorded only for a sample of about 25 sites.

**Appendix 5**
Spearman rank correlation coefficients comparing fluctuations in numbers on all sites counted every 2 h on 11 June 1976 and distances between plots*

| Study plot | Sites counted | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | U | S1 | S2 | S3 | S4 | Q1 | Q3 | Q4 | M | N | G1 | G4 |
| U | | 0.85 | 0.78 | 0.26 | 0.83 | 0.62 | 0.79 | 0.70 | 0.96 | 0.92 | 0.87 | 0.95 |
| S1 | 230 | | 0.62 | 0.17 | 0.98 | 0.46 | 0.95 | 0.58 | 0.89 | 0.85 | 0.94 | 0.85 |
| S2 | 230 | 0 | | 0.67 | 0.59 | 0.94 | 0.60 | 0.95 | 0.71 | 0.89 | 0.65 | 0.88 |
| S3 | 300 | 110 | 110 | | 0.12 | 0.78 | 0.11 | 0.79 | 0.09 | 0.46 | 0.14 | 0.37 |
| S4 | 300 | 110 | 110 | 0 | | 0.57 | 0.96 | 0.69 | 0.87 | 0.83 | 0.99 | 0.85 |
| Q1 | 440 | 220 | 220 | 150 | 150 | | 0.42 | 0.92 | 0.49 | 0.79 | 0.47 | 0.77 |
| Q3 | 410 | 190 | 190 | 110 | 110 | 50 | | 0.53 | 0.85 | 0.83 | 0.97 | 0.83 |
| Q4 | 440 | 220 | 220 | 150 | 150 | 20 | 30 | | 0.61 | 0.82 | 0.57 | 0.79 |
| M | 780 | 550 | 550 | 480 | 480 | 340 | 330 | 340 | | 0.88 | 0.91 | 0.88 |
| N | 730 | 500 | 500 | 440 | 440 | 300 | 370 | 300 | 50 | | 0.87 | 0.97 |
| G1 | 1950 | 1720 | 1720 | 1640 | 1640 | 1500 | 1530 | 1500 | 1170 | 1220 | | 0.89 |
| G4 | 1950 | 1720 | 1720 | 1640 | 1640 | 1500 | 1530 | 1500 | 1170 | 1220 | 20 | |

* Upper half, Spearman rank correlation coefficients ($r_s$).
Lower half, distances between plots in metres.

**Appendix 6**
Spearman rank correlation coefficients comparing fluctuations in numbers of birds counted on all sites every 2 h on 11 July 1976

| Study plot | Plots counted | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | U | S1 | S2 | S3 | S4 | Q1 | Q3 | Q4 | M | N | G1 | G4 |
| U | | 0.30 | 0.26 | 0.42 | 0.12 | 0.65 | 0.24 | 0.57 | 0.86 | 0.43 | 0.62 | 0.52 |
| S1 | | | 0.48 | 0.90 | 0.22 | 0.38 | 0.16 | 0.03 | 0.17 | 0.48 | 0.45 | 0.13 |
| S2 | | | | 0.34 | 0.55 | 0.27 | −0.59 | −0.34 | −0.14 | 0.77 | 0.33 | −0.25 |
| S3 | | | | | −0.02 | 0.59 | 0.30 | 0.29 | 0.44 | 0.51 | 0.53 | 0.07 |
| S4 | | | | | | 0.27 | −0.39 | −0.58 | −0.20 | 0.23 | −0.17 | −0.14 |
| Q1 | | | | | | | 0.21 | 0.31 | 0.60 | 0.61 | 0.33 | −0.04 |
| Q3 | | | | | | | | 0.55 | 0.77 | −0.35 | 0.41 | 0.62 |
| Q4 | | | | | | | | | 0.76 | 0.07 | 0.33 | 0.40 |
| M | | | | | | | | | | 0.15 | 0.66 | 0.62 |
| N | | | | | | | | | | | 0.44 | −0.25 |
| G1 | | | | | | | | | | | | 0.56 |
| G4 | | | | | | | | | | | | |

**Appendix 7**

Details of counts and conversion factors (*k*) used to calculate an estimate of the size of the breeding population of Thick-billed Murres at Prince Leopold Island in 1975*

| Area of cliff | Census date | No. of birds | *k* ratio | No. of breeding pairs | |
|---|---|---|---|---|---|
| | | | | Subtotals | Total |
| *East Cliff colony:* | | | | | |
| South spit to E: | 12 August | 9 000 | 0.76 | 6 840 | 6 840 |
| E to I | 5 August. | 24 877 | 0.73 | 18 160 | |
| | 5 August | 3 127 | 0.74 | 2 314 | |
| | 5 August | 4 954 | 0.73 | 3 616 | 24 090 |
| I to P | 9 August | 10 800 | 0.74 | 7 992 | |
| | 10 August | 2 946 | 0.78 | 2 298 | 10 290 |
| P to S | 6 August | 6 958 | 0.75 | 5 218 | |
| | 14 August | 9 300 | 0.77 | 7 161 | 12 379 |
| S to Z | 12 August | 4 800 | 0.76 | 3 648 | |
| | 14 August | 8 595 | 0.77 | 6 618 | 10 266 |
| Totals (East Cliff) | | 85 357 | | | 63 865 |
| *North Spit colony* | | | | | |
| Totals (North Spit) | 12 August | 8 600 | 0.77 | 6 536 | 6 536 |
| Grand totals (entire island) | | 93 957 | | | 70 401 |

* Counts made on 12 and 14 August 1975 are from photographs; all other counts are by direct observation.

**Appendix 8**

Details of counts of birds and conversion factors (*k*) used to calculate an estimate of the size of the breeding population of Thick-billed Murres at Prince Leopold Island for 1976–77*

| Area of cliff | Census date | No. of birds | *k* ratio | No. of breeding pairs | |
|---|---|---|---|---|---|
| | | | | Subtotals | Totals |
| *East Cliff colony:* | | | | | |
| South spit to E: | 21 July 1976 | 18 614 | 0.667 | 12 417 | |
| | 13 July 1977 | 3 556 | 0.790 | 2 808 | 15 225 |
| E to I | 21 July 1976 | 750 | 0.667 | 500 | |
| | 8 July 1977 | 3 670 | 0.766 | 2 811 | |
| | 16 July 1977 | 6 467 | 0.820 | 5 303 | |
| | 19 July 1977 | 5 993 | 0.700 | 4 195 | |
| | 21 July 1977 | 11 893 | 0.745 | 8 860 | |
| | 26 July 1977 | 3 496 | 0.625 | 2 185 | 23 854 |
| I to P | 21 July 1976 | 12 260 | 0.667 | 8 177 | 8 177 |
| P to S | 21July 1976 | 2 000 | 0.667 | 1 333 | |
| | 8 July 1977 | 9 284 | 0.766 | 7 110 | |
| | 12 July 1977 | 2 244 | 0.689 | 1 546 | |
| | 19 July 1977 | 5 562 | 0.700 | 3 898 | 13 887 |
| S to Z | 21 July 1976 | 10 697 | 0.667 | 7 135 | |
| | 9 July 1977 | 3 786 | 0.769 | 2 911 | 10 046 |
| Totals (East Cliff) | | 100 272 | | | 71 189 |
| *North Spit colony* | | | | | |
| Totals (North Spit) | 21 July 1976 | 19 629 | 0.667 | | 15 114 |
| Grand totals (entire island) | | 119 901 | | | 86 303 |

* Counts made on 21 July 1976 and 13 July 1977 are from photographs; all other counts are by direct observation.

**Appendix 9**

Breeding performance data for pairs of Thick-billed Murres on seven study plots along the East Cliff colony, 1975–77 (L = day egg laid, H = day egg hatched, F = day chick fledged; dates given are based on day 1 = 1 June, e.g., 26 = 26 June, 58 = 28 July, etc.)*

| | 1975 | | | | | | 1976 | | | | | | 1977 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | First egg | | | Relay | | | First egg | | | Relay | | | First egg | | | Relay | | |
| no. | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F |
| Plot G1: | | | | | | | | | | | | | | | | | | |
| 1 | 23 | — | — | — | — | — | 30 | 63 | 84 | — | — | — | 28 | 61 | — | — | — | — |
| 2 | 24 | — | — | ? | 85 | — | ? | 57 | 78 | — | — | — | 21 | 54 | 75 | — | — | — |
| 3 | 29 | — | — | — | — | — | 27 | — | — | — | — | — | 29 | 61 | 81 | — | — | — |
| 4 | ? | 56 | 77 | — | — | — | ? | 57 | 78 | — | — | — | ? | 64 | 84 | — | — | — |
| 5 | ? | 58 | 82 | — | — | — | ? | 62 | 79 | — | — | — | ? | 68 | 84 | — | — | — |
| 6 | ? | — | — | — | — | — | 27 | 57 | 76 | — | — | — | 27 | 62 | 84 | — | — | — |
| 7 | 26 | 58 | 82 | — | — | — | 23 | 57 | — | — | — | — | 24 | 56 | 75 | — | — | — |
| 8 | ? | 62 | 82 | — | — | — | 22 | 57 | 79 | — | — | — | ? | 67 | 88 | — | — | — |
| 9 | ? | 58 | 82 | — | — | — | 21 | 53 | 74 | — | — | — | 28 | 58 | 78 | — | — | — |
| 10 | ? | ? | 80 | — | — | — | 22 | 55 | 76 | — | — | — | 57 | — | — | — | — | — |
| 11 | ? | 58 | 85 | — | — | — | 20 | 51 | 74 | — | — | — | 25 | 56 | 78 | — | — | — |
| 12 | 25 | 56 | 80 | — | — | — | 23 | 57 | 79 | — | — | — | ? | 60 | 78 | — | — | — |
| 13 | ? | 60 | 77 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 14 | 31 | — | — | — | — | — | 27 | 58 | 78 | — | — | — | 47 | 79 | 98 | — | — | — |
| 15 | 23 | 55 | 77 | — | — | — | 26 | 58 | 79 | — | — | — | 28 | 60 | 81 | — | — | — |
| 16 | 30 | ? | 79 | — | — | — | 21 | 53 | 74 | — | — | — | 24 | 55 | 75 | — | — | — |
| 17 | 26 | 58 | 78 | — | — | — | ? | 58 | 74 | — | — | — | 25 | 57 | 75 | — | — | — |
| 18 | ? | ? | 92 | — | — | — | 21 | 62 | 79 | — | — | — | ? | — | — | ? | ? | 103 |
| 19 | ? | ? | 77 | — | — | — | ? | 62 | 79 | — | — | — | ? | 70 | 88 | — | — | — |
| 20 | 25 | 58 | 77 | — | — | — | 27 | 63 | 79 | — | — | — | ? | 66 | 84 | — | — | — |
| 21 | ? | ? | 84 | — | — | — | 23 | 55 | 78 | — | — | — | ? | 67 | 82 | — | — | — |
| 22 | ? | 58 | 82 | — | — | — | 27 | 57 | 79 | — | — | — | ? | — | — | — | — | — |
| 23 | ? | 58 | 79 | — | — | — | ? | 54 | 78 | — | — | — | 24 | 55 | 79 | — | — | — |
| 24 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 25 | ? | 66 | 87 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 26 | 50 | ? | 92 | — | — | — | 37 | — | — | — | — | — | 34 | 66 | 88 | — | — | — |
| 27 | ? | 61 | 82 | — | — | — | 30 | 63 | 84 | — | — | — | ? | 64 | 85 | — | — | — |
| 28 | ? | 62 | 84 | — | — | — | ? | 62 | 84 | — | — | — | 34 | 65 | 84 | — | — | — |
| 29 | ? | 62 | 85 | — | — | — | 28 | 62 | 84 | — | — | — | 39 | 68 | 94 | — | — | — |
| 30 | 45 | ? | 94 | — | — | — | ? | 74 | 95 | — | — | — | ? | 70 | 93 | — | — | — |
| 31 | 50 | ? | 94 | — | — | — | 48 | — | — | — | — | — | 39 | 71 | 93 | — | — | — |
| 32 | 25 | 56 | 78 | — | — | — | 25 | 57 | 79 | — | — | — | 44 | 74 | 98 | — | — | — |
| 33 | 25 | ? | 77 | — | — | — | ? | 62 | 80 | — | — | — | 31 | 64 | 83 | — | — | — |
| 34 | 25 | 58 | 77 | — | — | — | ? | — | — | — | — | — | ? | 61 | 84 | — | — | — |
| 35 | ? | 60 | 82 | — | — | — | 37 | 60 | 79 | — | — | — | ? | 65 | 84 | — | — | — |
| 36 | 28 | 60 | 84 | — | — | — | 25 | 58 | 80 | — | — | — | ? | 61 | 84 | — | — | — |
| 37 | 25 | 58 | 82 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 38 | ? | 63 | 87 | — | — | — | 30 | 62 | 79 | — | — | — | 39 | 68 | 88 | — | — | — |
| 39 | ? | 60 | 84 | — | — | — | 29 | 62 | 81 | — | — | — | 42 | — | — | — | — | — |
| 40 | 27 | 60 | 82 | — | — | — | 26 | 58 | 80 | — | — | — | 42 | — | — | — | — | — |
| 41 | 30 | 62 | 82 | — | — | — | ? | 56 | — | — | — | — | — | — | — | — | — | — |
| 42 | 31 | — | — | — | — | — | 30 | — | — | — | — | — | — | — | — | — | — | — |
| 43 | ? | ? | 85 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 44 | 25 | 60 | 78 | — | — | — | 26 | 58 | 79 | — | — | — | ? | 64 | 85 | — | — | — |
| 45 | ? | ? | 86 | — | — | — | ? | 58 | 79 | — | — | — | ? | 65 | 88 | — | — | — |
| 46 | ? | ? | 79 | — | — | — | ? | 58 | 79 | — | — | — | ? | ? | ? | — | — | — |
| 47 | 25 | 56 | 77 | — | — | — | 26 | 57 | 79 | — | — | — | 25 | — | — | 43 | — | — |
| 48 | ? | 58 | 77 | — | — | — | ? | 50 | 74 | — | — | — | 27 | 58 | 79 | — | — | — |
| 49 | 29 | 60 | 82 | — | — | — | ? | 58 | 79 | — | — | — | 26 | — | — | ? | ? | 94 |
| 50 | ? | 60 | 78 | — | — | — | 23 | 55 | 76 | — | — | — | 29 | 57 | 78 | — | — | — |
| 51 | ? | 79 | 96 | — | — | — | 28 | — | — | 48 | 68 | 94 | 33 | 64 | 84 | — | — | — |
| 52 | 28 | 61 | 82 | — | — | — | ? | 53 | 76 | — | — | — | 44 | 76 | 94 | — | — | — |
| 54 | — | — | — | — | — | — | ? | 56 | 79 | — | — | — | 31 | 62 | 85 | — | — | — |
| 55 | ? | 73 | 92 | — | — | — | 28 | 58 | 79 | — | — | — | 29 | 62 | 83 | — | — | — |
| 62 | — | — | — | — | — | — | ? | — | — | 43 | — | — | 31 | 66 | 84 | — | — | — |
| 64 | — | — | — | — | — | — | ? | 62 | 81 | — | — | — | ? | 65 | 100 | — | — | — |
| 65 | ? | 62 | 85 | — | — | — | ? | 62 | 81 | — | — | — | 43 | 74 | 93 | — | — | — |
| 68 | — | — | — | — | — | — | 43 | — | — | — | — | — | — | — | — | — | — | — |
| 71 | — | — | — | — | — | — | ? | 81 | 99 | — | — | — | — | — | — | — | — | — |
| 72 | ? | 58 | 79 | — | — | — | — | — | — | — | — | — | ? | 62 | 84 | — | — | — |
| 74 | — | — | — | — | — | — | — | — | — | — | — | — | 43 | ? | 94 | — | — | — |
| 85 | — | — | — | — | — | — | — | — | — | — | — | — | ? | — | — | — | — | — |

**Appendix 9** (cont'd)

| Site | 1975 | | | | | | 1976 | | | | | | 1977 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | First egg | | | Relay | | | First egg | | | Relay | | | First egg | | | Relay | | |
| no. | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F |
| Plot G4: | | | | | | | | | | | | | | | | | | |
| 1 | 25 | 60 | 82 | — | — | — | ? | 54 | 79 | — | — | — | 29 | — | — | — | — | — |
| 2 | 29 | — | — | — | — | — | ? | 57 | 79 | — | — | — | ? | 59 | 79 | — | — | — |
| 3 | ? | 55 | 73 | — | — | — | ? | 58 | 75 | — | — | — | ? | 58 | 78 | — | — | — |
| 4 | ? | 62 | 82 | — | — | — | ? | 54 | 79 | — | — | — | ? | 56 | 78 | — | — | — |
| 5 | ? | 61 | 82 | — | — | — | 28 | 65 | 81 | — | — | — | 30 | 61 | 82 | — | — | — |
| 6 | ? | 62 | 86 | — | — | — | 31 | 63 | 83 | — | — | — | 33 | 65 | 84 | — | — | — |
| 7 | ? | 62 | 77 | — | — | — | 31 | 54 | 78 | — | — | — | 26 | 56 | 77 | — | — | — |
| 8 | 26 | 56 | 77 | — | — | — | 28 | 53 | 74 | — | — | — | 26 | 59 | 78 | — | — | — |
| 9 | ? | 58 | 77 | — | — | — | 23 | 64 | — | — | — | — | 44 | 75 | 94 | — | — | — |
| 10 | ? | ? | 87 | — | — | — | ? | 55 | 79 | — | — | — | 25 | 58 | 78 | — | — | — |
| 11 | 23 | 55 | 73 | — | — | — | ? | 50 | 70 | — | — | — | ? | 60 | 82 | — | — | — |
| 12 | ? | — | — | — | — | — | 25 | — | — | — | — | — | ? | — | — | — | — | — |
| 13 | ? | 58 | 77 | — | — | — | ? | 58 | 81 | — | — | — | ? | 68 | 89 | — | — | — |
| 14 | ? | 56 | 74 | — | — | — | — | — | — | — | — | — | ? | 84 | — | — | — | — |
| 15 | 23 | — | — | 38 | 71 | 88 | — | — | — | — | — | — | 31 | — | — | ? | — | — |
| 16 | ? | 58 | 74 | — | — | — | — | — | — | — | — | — | 51 | — | — | — | — | — |
| 17 | 27 | — | — | — | — | — | 29 | — | — | — | — | — | — | — | — | — | — | — |
| 18 | 25 | 55 | 74 | — | — | — | 22 | 50 | 71 | — | — | — | ? | 60 | 79 | — | — | — |
| 19 | ? | 56 | ? | — | — | — | ? | ? | — | — | — | — | ? | 60 | — | — | — | — |
| 20 | ? | 60 | 79 | — | — | — | ? | 62 | 79 | — | — | — | — | — | — | — | — | — |
| 21 | — | — | — | — | — | — | 30 | 58 | 84 | — | — | — | 33 | — | — | — | — | — |
| 22 | ? | 60 | 84 | — | — | — | 29 | — | — | — | — | — | — | — | — | — | — | — |
| 23 | ? | ? | 82 | — | — | — | ? | 57 | 82 | — | — | — | 41 | — | — | — | — | — |
| 24 | ? | ? | 77 | — | — | — | ? | 57 | 79 | — | — | — | 29 | — | — | 44 | — | — |
| 25 | ? | 56 | 73 | — | — | — | 23 | 53 | 79 | — | — | — | ? | 57 | 79 | — | — | — |
| 26 | 26 | ? | 77 | — | — | — | 28 | 53 | 79 | — | — | — | — | — | — | — | — | — |
| 27 | ? | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 28 | 26 | 58 | — | — | — | — | 36 | — | — | — | — | — | 29 | 61 | 79 | — | — | — |
| 29 | ? | 58 | 77 | — | — | — | ? | 64 | 82 | — | — | — | ? | 66 | 85 | — | — | — |
| 30 | ? | 60 | 77 | — | — | — | ? | 55 | 74 | — | — | — | 26 | — | — | 65 | — | — |
| 31 | ? | ? | 94 | — | — | — | 39 | — | — | — | — | — | — | — | — | — | — | — |
| 32 | 28 | ? | 79 | — | — | — | 29 | 57 | 76 | — | — | — | ? | 58 | 78 | — | — | — |
| 33 | ? | — | — | — | — | — | 22 | 53 | 75 | — | — | — | 39 | — | — | — | — | — |
| 34 | 26 | 56 | 79 | — | — | — | 24 | 57 | 79 | — | — | — | 24 | 57 | 82 | — | — | — |
| 35 | 29 | 61 | 85 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 36 | 26 | 56 | 77 | — | — | — | 21 | 50 | 69 | — | — | — | 29 | — | — | — | — | — |
| 37 | 25 | 56 | 77 | — | — | — | ? | 57 | 82 | — | — | — | 29 | 61 | 82 | — | — | — |
| 38 | ? | ? | 77 | — | — | — | 26 | 64 | — | — | — | — | — | — | — | — | — | — |
| 39 | 25 | 58 | 77 | — | — | — | 24 | 57 | 79 | — | — | — | — | — | — | — | — | — |
| 40 | 29 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 41 | 23 | 55 | 74 | — | — | — | 22 | — | — | — | — | — | 21 | 53 | 75 | — | — | — |
| 42 | ? | 62 | 79 | — | — | — | 45 | — | — | — | — | — | ? | — | — | — | — | — |
| 43 | ? | — | — | — | — | — | ? | 66 | 84 | — | — | — | ? | — | — | — | — | — |
| 44 | ? | 62 | 80 | — | — | — | ? | 67 | — | — | — | — | 23 | 55 | 78 | — | — | — |
| 45 | 29 | — | — | — | — | — | 53 | — | — | — | — | — | ? | — | — | — | — | — |
| 46 | ? | 61 | 84 | — | — | — | 26 | 58 | 83 | — | — | — | 30 | 61 | 82 | — | — | — |
| 47 | ? | 67 | — | — | — | — | 27 | 55 | 79 | — | — | — | 29 | 61 | — | — | — | — |
| 48 | ? | 61 | 84 | — | — | — | 37 | — | — | — | — | — | 31 | 66 | 88 | — | — | — |
| 49 | ? | 57 | 78 | — | — | — | 33 | 63 | 82 | — | — | — | 32 | 65 | 84 | — | — | — |
| 50 | ? | 62 | 80 | — | — | — | ? | — | — | — | — | — | 59 | — | — | — | — | — |
| 51 | 25 | 56 | 78 | — | — | — | ? | 69 | — | — | — | — | 28 | 60 | 82 | — | — | — |
| 52 | ? | — | — | — | — | — | 30 | — | — | — | — | — | 36 | — | — | — | — | — |
| 53 | 27 | — | 94 | — | — | — | 23 | 55 | 79 | — | — | — | 31 | 64 | 84 | — | — | — |
| 54 | 25 | — | — | — | — | — | ? | 62 | 81 | — | — | — | ? | — | — | — | — | — |
| 55 | — | — | — | — | — | — | ? | ? | 77 | — | — | — | 29 | — | — | — | — | — |
| 56 | — | — | — | — | — | — | ? | 61 | 79 | — | — | — | 31 | 64 | 84 | — | — | — |
| 57 | 29 | 60 | 79 | — | — | — | ? | — | — | — | — | — | 31 | — | — | — | — | — |
| 58 | ? | ? | 79 | — | — | — | ? | 53 | 81 | — | — | — | ? | 67 | 88 | — | — | — |
| 59 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | — | — | — | — | — |
| 60 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | 58 | — | — | — | — |
| 61 | 27 | — | — | — | — | — | ? | 67 | 82 | — | — | — | ? | — | — | — | — | — |
| 62 | ? | — | — | — | — | — | ? | — | — | — | — | — | 51 | 83 | — | — | — | — |

**Appendix 9** (cont'd)

| Site no. | 1975 | | | | | | 1976 | | | | | | 1977 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | First egg | | | Relay | | | First egg | | | Relay | | | First egg | | | Relay | | |
| | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F |
| 63 | — | — | — | — | — | — | ? | 54 | 76 | — | — | — | ? | 62 | 84 | — | — | — |
| 64 | — | — | — | — | — | — | ? | 73 | 89 | — | — | — | 26 | — | — | ? | 75 | 94 |
| 65 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 66 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 67 | — | — | — | — | — | — | 34 | 67 | 82 | — | — | — | ? | 70 | 93 | — | — | — |
| 68 | — | — | — | — | — | — | ? | — | — | — | — | — | 37 | 68 | 85 | — | — | — |
| 70 | — | — | — | — | — | — | 39 | — | — | — | — | — | ? | 68 | 88 | — | — | — |
| 72 | — | — | — | — | — | — | ? | 69 | 87 | — | — | — | 36 | 69 | 92 | — | — | — |
| 75 | — | — | — | — | — | — | 46 | — | — | — | — | — | 42 | — | — | — | — | — |
| 77 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 79 | ? | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 80 | — | — | — | — | — | — | — | — | — | — | — | — | 33 | 66 | 86 | — | — | — |
| 82 | — | — | — | — | — | — | — | — | — | — | — | — | ? | 71 | 91 | — | — | — |
| 83 | — | — | — | — | — | — | — | — | — | — | — | — | 29 | 60 | 83 | — | — | — |
| 87 | — | — | — | — | — | — | — | — | — | — | — | — | 39 | — | — | — | — | — |
| 89 | — | — | — | — | — | — | — | — | — | — | — | — | ? | ? | — | — | — | — |
| 93 | — | — | — | — | — | — | — | — | — | — | — | — | ? | 69 | 88 | — | — | — |
| 94 | — | — | — | — | — | — | — | — | — | — | — | — | ? | — | — | — | — | — |
| Plot N: | | | | | | | | | | | | | | | | | | |
| 1 | ? | 63 | 84 | — | — | — | ? | 58 | 82 | — | — | — | ? | 68 | 89 | — | — | — |
| 2 | ? | — | — | ? | — | — | ? | 61 | 82 | — | — | — | ? | 62 | 84 | — | — | — |
| 3 | ? | — | — | ? | 81 | ? | ? | 61 | 89 | — | — | — | ? | 60 | 82 | — | — | — |
| 4 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 5 | 27 | 61 | 80 | — | — | — | 25 | 56 | 88 | — | — | — | ? | 60 | 84 | — | — | — |
| 6 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 7 | ? | 62 | 82 | — | — | — | 26 | 57 | 80 | — | — | — | ? | 62 | 82 | — | — | — |
| 8 | ? | — | — | — | — | — | ? | 61 | 82 | — | — | — | 35 | 66 | 85 | — | — | — |
| 9 | 28 | 62 | 81 | — | — | — | ? | 53 | 77 | — | — | — | ? | 51 | — | — | — | — |
| 10 | 29 | 62 | 79 | — | — | — | ? | 58 | 77 | — | — | — | 35 | 65 | 84 | — | — | — |
| 11 | ? | 64 | — | — | — | — | ? | 58 | 77 | — | — | — | ? | 66 | 84 | — | — | — |
| 12 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 13 | ? | 62 | 81 | — | — | — | 24 | 61 | 82 | — | — | — | — | — | — | — | — | — |
| 14 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 15 | ? | 65 | 87 | — | — | — | ? | 58 | 82 | — | — | — | 30 | 62 | 82 | — | — | — |
| 16 | ? | ? | 87 | — | — | — | ? | ? | 83 | — | — | — | ? | 67 | 88 | — | — | — |
| 17 | — | — | — | — | — | — | ? | 61 | 81 | — | — | — | ? | 74 | 94 | — | — | — |
| 18 | 27 | 62 | 79 | — | — | — | ? | — | — | — | — | — | 30 | ? | 84 | — | — | — |
| 19 | ? | 58 | 79 | — | — | — | ? | 56 | 78 | — | — | — | 35 | 67 | 84 | — | — | — |
| 20 | — | — | — | — | — | — | 38 | — | — | — | — | — | ? | 69 | 90 | — | — | — |
| 21 | 27 | 62 | 79 | — | — | — | 25 | 57 | 78 | — | — | — | ? | 59 | 84 | — | — | — |
| 22 | ? | 67 | 87 | — | — | — | 30 | ? | 82 | — | — | — | 30 | 62 | 82 | — | — | — |
| 23 | ? | 65 | 87 | — | — | — | 25 | 56 | 78 | — | — | — | 30 | ? | 84 | — | — | — |
| 24 | ? | — | — | — | — | — | ? | 56 | — | — | — | — | ? | 81 | 98 | — | — | — |
| 25 | 25 | 58 | 83 | — | — | — | 27 | ? | 83 | — | — | — | ? | ? | 84 | — | — | — |
| 26 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | ? | 84 | — | — | — |
| 27 | ? | 64 | 82 | — | — | — | ? | 61 | 83 | — | — | — | ? | ? | 84 | — | — | — |
| 28 | 29 | 59 | 82 | — | — | — | ? | — | — | 48 | 72 | — | ? | ? | 84 | — | — | — |
| 29 | ? | 65 | 86 | — | — | — | ? | ? | 89 | — | — | — | ? | 69 | 89 | — | — | — |
| 30 | 28 | 62 | 81 | — | — | — | ? | 58 | 82 | — | — | — | ? | 66 | 85 | — | — | — |
| 31 | 29 | 62 | 83 | — | — | — | ? | 58 | 82 | — | — | — | ? | ? | 84 | — | — | — |
| 32 | 26 | 56 | 77 | — | — | — | ? | 55 | 78 | — | — | — | ? | 59 | 82 | — | — | — |
| 33 | ? | 64 | 84 | — | — | — | 30 | ? | 84 | — | — | — | ? | 67 | 88 | — | — | — |
| 34 | ? | 56 | — | — | — | — | ? | 61 | 83 | — | — | — | ? | — | — | — | — | — |
| 35 | 28 | 58 | 77 | — | — | — | ? | 55 | 79 | — | — | — | ? | 61 | — | — | — | — |
| 36 | ? | 58 | 79 | — | — | — | 26 | 51 | 82 | — | — | — | ? | ? | 84 | — | — | — |
| 37 | ? | 58 | 78 | — | — | — | ? | 51 | 78 | — | — | — | ? | — | — | — | — | — |
| 38 | 25 | 59 | 77 | — | — | — | ? | 61 | 83 | — | — | — | ? | 66 | 84 | — | — | — |
| 39 | 28 | ? | ? | — | — | — | 27 | 61 | 82 | — | — | — | ? | ? | — | — | — | — |
| 40 | 26 | 58 | 77 | — | — | — | ? | 58 | 82 | — | — | — | ? | — | — | — | — | — |
| 41 | 26 | — | — | — | — | — | 27 | — | — | ? | 82 | 100 | ? | 74 | 94 | — | — | — |
| 42 | ? | — | — | — | — | — | 31 | 68 | 87 | — | — | — | ? | 68 | 88 | — | — | — |

**Appendix 9** (cont'd)

| Site no. | 1975 | | | | | | 1976 | | | | | | 1977 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | First egg | | | Relay | | | First egg | | | Relay | | | First egg | | | Relay | | |
| | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F |
| 44 | ? | 64 | 87 | — | — | — | ? | 61 | 84 | — | — | — | ? | 67 | 89 | — | — | — |
| 45 | 26 | 56 | 77 | — | — | — | ? | 57 | 74 | — | — | — | ? | 65 | 88 | — | — | — |
| 46 | ? | 56 | 77 | — | — | — | ? | 57 | 78 | — | — | — | ? | 65 | 82 | — | — | — |
| 47 | 26 | 58 | 84 | — | — | — | ? | 56 | 77 | — | — | — | ? | 60 | 82 | — | — | — |
| 48 | 26 | 56 | 78 | — | — | — | ? | 58 | 78 | — | — | — | ? | 61 | 82 | — | — | — |
| 49 | ? | 55 | 77 | — | — | — | ? | 55 | 77 | — | — | — | ? | 66 | 84 | — | — | — |
| 50 | ? | 56 | 74 | — | — | — | 23 | 56 | 81 | — | — | — | ? | 60 | 84 | — | — | — |
| 51 | ? | 58 | 77 | — | — | — | ? | 57 | — | — | — | — | ? | — | — | — | — | — |
| 52 | 28 | ? | 83 | — | — | — | 25 | 53 | 75 | — | — | — | ? | 58 | 82 | — | — | — |
| 53 | ? | ? | 87 | — | — | — | ? | ? | 87 | — | — | — | ? | ? | 84 | — | — | — |
| 54 | 26 | 59 | 83 | — | — | — | ? | 54 | 80 | — | — | — | ? | 69 | 88 | — | — | — |
| 55 | ? | 62 | 84 | — | — | — | ? | 56 | 83 | — | — | — | ? | 66 | 88 | — | — | — |
| 56 | 28 | 59 | 82 | — | — | — | ? | 61 | 80 | — | — | — | ? | — | — | — | — | — |
| 57 | ? | 64 | 87 | — | — | — | ? | 68 | 84 | — | — | — | ? | — | — | — | — | — |
| 58 | ? | 67 | 91 | — | — | — | ? | 61 | 89 | — | — | — | ? | 69 | 90 | — | — | — |
| 59 | — | — | — | — | — | — | 18 | 61 | 83 | — | — | — | ? | 66 | 88 | — | — | — |
| 60 | ? | 64 | 84 | — | — | — | ? | 56 | 79 | — | — | — | ? | 61 | 84 | — | — | — |
| 61 | 25 | 58 | 77 | — | — | — | 27 | 61 | 77 | — | — | — | ? | 66 | 82 | — | — | — |
| 62 | — | — | — | — | — | — | ? | 61 | — | — | — | — | ? | ? | 84 | — | — | — |
| 63 | ? | 62 | 81 | — | — | — | ? | 58 | 80 | — | — | — | ? | 62 | 84 | — | — | — |
| 64 | ? | 62 | 81 | — | — | — | ? | 58 | 79 | — | — | — | ? | 59 | 82 | — | — | — |
| 65 | 26 | 58 | 82 | — | — | — | ? | 61 | 82 | — | — | — | ? | — | — | — | — | — |
| 66 | ? | 65 | 87 | — | — | — | ? | 59 | 82 | — | — | — | 30 | ? | 84 | — | — | — |
| 67 | ? | — | — | ? | 62 | 85 | ? | 61 | 82 | — | — | — | ? | 61 | 82 | — | — | — |
| 68 | 26 | 59 | 83 | — | — | — | — | — | — | — | — | — | ? | — | — | — | — | — |
| 69 | ? | 62 | 83 | — | — | — | 27 | 61 | 82 | — | — | — | ? | 65 | 84 | — | — | — |
| 70 | 25 | 56 | 77 | — | — | — | ? | 68 | 89 | — | — | — | ? | 61 | 84 | — | — | — |
| 71 | — | — | — | — | — | — | 42 | — | — | — | — | — | — | — | — | — | — | — |
| 72 | ? | — | — | — | — | — | ? | 61 | 80 | — | — | — | ? | 61 | 82 | — | — | — |
| 73 | — | — | — | — | — | — | ? | 61 | 82 | — | — | — | — | — | — | — | — | — |
| 74 | ? | 67 | 84 | — | — | — | ? | 61 | 91 | — | — | — | ? | 70 | 89 | — | — | — |
| 75 | ? | 56 | — | — | — | — | ? | 61 | 91 | — | — | — | ? | 68 | 89 | — | — | — |
| 76 | ? | 67 | 82 | — | — | — | ? | 58 | 82 | — | — | — | ? | 68 | 89 | — | — | — |
| 77 | ? | 56 | — | — | — | — | 37 | 61 | 89 | — | — | — | ? | 76 | 94 | — | — | — |
| 78 | ? | 63 | 85 | — | — | — | ? | ? | 82 | — | — | — | 37 | 68 | 84 | — | — | — |
| 79 | ? | — | — | — | — | — | ? | 61 | 83 | — | — | — | ? | 67 | 89 | — | — | — |
| 80 | — | — | — | — | — | — | 34 | ? | 87 | — | — | — | — | — | — | — | — | — |
| 81 | ? | 73 | 91 | — | — | — | ? | 72 | 90 | — | — | — | ? | 66 | 88 | — | — | — |
| 82 | 27 | 58 | 78 | — | — | — | ? | 70 | — | — | — | — | 36 | — | — | — | — | — |
| 83 | — | — | — | — | — | — | ? | 58 | 78 | — | — | — | ? | 59 | 82 | — | — | — |
| 84 | — | — | — | — | — | — | 34 | — | — | 53 | — | — | — | — | — | — | — | — |
| 85 | — | — | — | — | — | — | ? | 72 | 89 | — | — | — | 36 | 68 | 88 | — | — | — |
| 86 | ? | 63 | 87 | — | — | — | ? | 56 | 73 | — | — | — | ? | 65 | 84 | — | — | — |
| 87 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | — | — | — | — | — |
| 88 | ? | 67 | 87 | — | — | — | ? | 68 | — | — | — | — | — | — | — | — | — | — |
| 89 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 90 | ? | 62 | 82 | — | — | — | ? | 53 | 77 | — | — | — | 25 | 61 | 84 | — | — | — |
| 91 | ? | ? | 87 | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 93 | — | — | — | — | — | — | ? | 56 | 79 | — | — | — | ? | — | — | — | — | — |
| 95 | ? | — | — | — | — | — | ? | 61 | 84 | — | — | — | ? | 67 | 88 | — | — | — |
| 96 | ? | 59 | 79 | — | — | — | ? | 58 | 82 | — | — | — | ? | 65 | 84 | — | — | — |
| 97 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 98 | ? | 62 | 84 | — | — | — | 48 | 80 | — | — | — | — | 36 | — | — | — | — | — |
| 99 | — | — | — | — | — | — | ? | 68 | — | — | — | — | ? | 67 | 85 | — | — | — |
| 103 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | 74 | — | — | — | — |
| 104 | — | — | — | — | — | — | ? | — | 87 | — | — | — | 46 | ? | 98 | — | — | — |
| 105 | — | — | — | — | — | — | ? | 72 | — | — | — | — | ? | 76 | 94 | — | — | — |
| 106 | — | — | — | — | — | — | ? | 68 | 84 | — | — | — | — | — | — | — | — | — |
| 107 | ? | 62 | 87 | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 108 | 28 | 58 | 82 | — | — | — | ? | 58 | 76 | — | — | — | ? | 56 | 75 | — | — | — |
| 109 | ? | 64 | 86 | — | — | — | ? | 72 | — | — | — | — | ? | — | — | — | — | — |
| 110 | — | — | — | — | — | — | ? | 74 | 94 | — | — | — | ? | 68 | 89 | — | — | — |
| 111 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | — | — | — | — | — |

**Appendix 9** (cont'd)

| Site no. | 1975 | | | | | | 1976 | | | | | | 1977 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | First egg | | | Relay | | | First egg | | | Relay | | | First egg | | | Relay | | |
| | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F |
| 116 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 117 | 26 | 59 | 83 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 118 | 29 | 62 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 121 | — | — | — | — | — | — | — | — | — | — | — | — | ? | — | — | — | — | — |
| 122 | — | — | — | — | — | — | — | — | — | — | — | — | ? | 59 | 83 | — | — | — |
| 125 | — | — | — | — | — | — | — | — | — | — | — | — | ? | 81 | 98 | — | — | — |
| 126 | — | — | — | — | — | — | — | — | — | — | — | — | ? | 68 | 88 | — | — | — |
| 127 | — | — | — | — | — | — | — | — | — | — | — | — | ? | 62 | 84 | — | — | — |
| Plot Q1: | | | | | | | | | | | | | | | | | | |
| 1 | 24 | — | — | — | — | — | 22 | — | — | 36 | 65 | 84 | ? | — | — | — | — | — |
| 2 | 28 | 60 | 79 | — | — | — | ? | 73 | — | — | — | — | ? | 61 | 82 | — | — | — |
| 3 | ? | 60 | 82 | — | — | — | 32 | — | — | — | — | — | ? | — | — | — | — | — |
| 4 | ? | 60 | — | — | — | — | 25 | — | — | — | — | — | ? | 70 | 90 | — | — | — |
| 5 | ? | 67 | 84 | — | — | — | ? | — | — | — | — | — | ? | 66 | 83 | — | — | — |
| 6 | ? | ? | 79 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 7 | 26 | 57 | 77 | — | — | — | ? | 56 | 79 | — | — | — | ? | 76 | — | — | — | — |
| 8 | ? | 67 | 83 | — | — | — | 26 | 73 | — | — | — | — | ? | 61 | 81 | — | — | — |
| 9 | 23 | 55 | 75 | — | — | — | ? | 63 | 81 | — | — | — | ? | 62 | 82 | — | — | — |
| 10 | 28 | 61 | 82 | — | — | — | ? | — | — | — | — | — | ? | 60 | 85 | — | — | — |
| 11 | ? | 61 | 82 | — | — | — | ? | — | — | — | — | — | ? | 60 | 88 | — | — | — |
| 12 | ? | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 13 | 29 | — | — | ? | 76 | — | ? | ? | 84 | — | — | — | ? | 61 | 84 | — | — | — |
| 14 | ? | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 15 | ? | 71 | ? | — | — | — | — | — | — | — | — | — | ? | 65 | 84 | — | — | — |
| 16 | 25 | 57 | 77 | — | — | — | ? | — | — | 42 | 80 | — | 37 | 68 | 89 | — | — | — |
| 17 | ? | 65 | 88 | — | — | — | 28 | — | — | — | — | — | ? | 58 | — | — | — | — |
| 18 | ? | 65 | 87 | — | — | — | ? | — | — | — | — | — | ? | 61 | 85 | — | — | — |
| 19 | ? | 67 | 87 | — | — | — | 37 | — | — | — | — | — | ? | 67 | 85 | — | — | — |
| 20 | ? | — | — | — | — | — | 32 | — | — | — | — | — | ? | — | — | — | — | — |
| 21 | 28 | — | — | ? | 76 | — | — | — | — | — | — | — | ? | 79 | 93 | — | — | — |
| 22 | 28 | 61 | 84 | — | — | — | 32 | — | — | ? | 80 | — | ? | 68 | 83 | — | — | — |
| 23 | ? | — | — | — | — | — | ? | — | — | — | — | — | ? | 69 | 84 | — | — | — |
| 24 | 26 | — | — | — | — | — | 22 | — | — | — | — | — | 24 | — | — | — | — | — |
| 25 | ? | 67 | — | — | — | — | 32 | — | — | — | — | — | 35 | 68 | 88 | — | — | — |
| 26 | ? | 67 | 84 | — | — | — | 29 | ? | 80 | — | — | — | ? | 72 | 89 | — | — | — |
| 27 | ? | 64 | 86 | — | — | — | 26 | — | — | — | — | — | ? | 60 | 84 | — | — | — |
| 28 | ? | 61 | 84 | — | — | — | 35 | — | — | — | — | — | — | — | — | — | — | — |
| 29 | ? | 64 | 84 | — | — | — | ? | — | — | — | — | — | ? | — | — | ? | 71 | 92 |
| 30 | ? | 61 | 82 | — | — | — | ? | — | — | — | — | — | ? | 68 | — | — | — | — |
| 31 | ? | 61 | 81 | — | — | — | ? | — | — | — | — | — | ? | 67 | 85 | — | — | — |
| 32 | ? | 67 | 83 | — | — | — | 32 | — | — | — | — | — | ? | 67 | 85 | — | — | — |
| 33 | ? | 59 | 77 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 34 | — | — | — | — | — | — | — | — | — | — | — | — | 37 | 68 | 89 | — | — | — |
| 35 | ? | 67 | — | — | — | — | 28 | 69 | — | — | — | — | ? | 79 | 99 | — | — | — |
| 36 | 26 | 57 | 77 | — | — | — | 32 | 69 | — | — | — | — | ? | 65 | 84 | — | — | — |
| 37 | ? | 67 | ? | — | — | — | 30 | 63 | 83 | — | — | — | ? | 65 | 82 | — | — | — |
| 38 | ? | ? | 79 | — | — | — | ? | 63 | 83 | — | — | — | ? | 69 | 88 | — | — | — |
| 39 | ? | 59 | 88 | — | — | — | 32 | ? | 84 | — | — | — | ? | 68 | 85 | — | — | — |
| 40 | ? | 61 | 77 | — | — | — | ? | ? | 84 | — | — | — | 26 | 61 | 82 | — | — | — |
| 41 | ? | 61 | 81 | — | — | — | ? | ? | 82 | — | — | — | ? | 68 | 88 | — | — | — |
| 42 | ? | 61 | 77 | — | — | — | 28 | 69 | — | — | — | — | ? | 65 | 84 | — | — | — |
| 43 | ? | 61 | 85 | — | — | — | 29 | 63 | 83 | — | — | — | ? | 60 | 82 | — | — | — |
| 44 | ? | 64 | 82 | — | — | — | 26 | — | — | — | — | — | ? | 61 | 82 | — | — | — |
| 45 | 27 | 61 | 78 | — | — | — | — | — | — | — | — | — | ? | 65 | 82 | — | — | — |
| 46 | ? | 65 | 86 | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 47 | 23 | 55 | 74 | — | — | — | ? | — | — | — | — | — | ? | 60 | 78 | — | — | — |
| 48 | ? | 67 | — | — | — | — | 52 | 79 | — | — | — | — | — | — | — | — | — | — |
| 49 | 28 | 57 | 77 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 50 | ? | 61 | 84 | — | — | — | 22 | — | — | — | — | — | 44 | 74 | 93 | — | — | — |
| 51 | ? | — | — | ? | 78 | — | 32 | — | — | — | — | — | 39 | — | — | — | — | — |
| 52 | ? | 64 | 83 | — | — | — | ? | 69 | — | — | — | — | ? | 66 | — | — | — | — |
| 53 | 28 | 61 | 77 | — | — | — | ? | 69 | — | — | — | — | ? | — | — | — | — | — |

**Appendix 9** (cont'd)

| Site no. | 1975 | | | | | | 1976 | | | | | | 1977 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | First egg | | | Relay | | | First egg | | | Relay | | | First egg | | | Relay | | |
| | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F |
| 54 | ? | 61 | 82 | — | — | — | 30 | 63 | 82 | — | — | — | ? | 65 | 84 | — | — | — |
| 55 | ? | 61 | 79 | — | — | — | 25 | — | — | — | — | — | ? | 61 | 81 | — | — | — |
| 56 | ? | 65 | — | — | — | — | 29 | — | — | 36 | — | — | 40 | 72 | 90 | — | — | — |
| 57 | ? | 61 | 77 | — | — | — | 29 | — | — | 56 | — | — | ? | 64 | 88 | — | — | — |
| 58 | ? | 59 | 79 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 59 | ? | 61 | ? | — | — | — | ? | 67 | 84 | — | — | — | ? | 66 | 88 | — | — | — |
| 60 | ? | 64 | 85 | — | — | — | 36 | 67 | 84 | — | — | — | ? | — | — | — | — | — |
| 61 | ? | 61 | 81 | — | — | — | ? | — | — | — | — | — | ? | — | — | — | — | — |
| 62 | 27 | 61 | 82 | — | — | — | 22 | — | — | ? | 72 | — | — | — | — | — | — | — |
| 63 | ? | 61 | 78 | — | — | — | ? | ? | — | — | — | — | ? | — | — | — | — | — |
| 64 | ? | 61 | 84 | — | — | — | ? | — | — | — | — | — | ? | 65 | 84 | — | — | — |
| 65 | ? | 61 | 87 | — | — | — | ? | 73 | — | — | — | — | ? | 67 | 85 | — | — | — |
| 66 | ? | 67 | 87 | — | — | — | ? | — | — | 63 | — | — | ? | 65 | 84 | — | — | — |
| 67 | — | — | — | — | — | — | ? | 77 | — | — | — | — | — | — | — | — | — | — |
| 68 | ? | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 69 | 27 | ? | 83 | — | — | — | ? | — | — | — | — | — | ? | — | — | — | — | — |
| 70 | ? | 57 | 77 | — | — | — | 25 | 56 | 77 | — | — | — | ? | 56 | 78 | — | — | — |
| 71 | 27 | — | — | ? | 73 | — | ? | 74 | 94 | — | — | — | 24 | 56 | 75 | — | — | — |
| 72 | ? | 61 | 84 | — | — | — | — | — | — | — | — | — | ? | — | — | — | — | — |
| 73 | ? | 67 | 84 | — | — | — | ? | 57 | 81 | — | — | — | ? | 67 | — | — | — | — |
| 74 | 26 | 57 | 78 | — | — | — | ? | 57 | 79 | — | — | — | ? | 58 | 79 | — | — | — |
| 75 | — | — | — | — | — | — | 36 | — | — | ? | 73 | 94 | ? | — | — | — | — | — |
| 76 | ? | 61 | 81 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 77 | — | — | — | — | — | — | ? | 69 | — | — | — | — | 28 | — | — | — | — | — |
| 78 | 28 | 60 | 82 | — | — | — | ? | — | — | — | — | — | ? | — | — | ? | ? | — |
| 79 | ? | 67 | ? | — | — | — | 22 | 52 | 74 | — | — | — | ? | 64 | 81 | — | — | — |
| 80 | ? | 67 | 87 | — | — | — | ? | 55 | 78 | — | — | — | ? | 69 | 89 | — | — | — |
| 81 | ? | 65 | 83 | — | — | — | ? | 57 | 81 | — | — | — | ? | — | — | — | — | — |
| 83 | ? | 65 | 82 | — | — | — | 26 | 53 | 82 | — | — | — | ? | 68 | 84 | — | — | — |
| 84 | 28 | 61 | 78 | — | — | — | ? | 56 | 78 | — | — | — | 39 | 71 | 93 | — | — | — |
| 86 | 26 | ? | 79 | — | — | — | 22 | — | — | 36 | — | — | ? | 60 | 84 | — | — | — |
| 87 | 29 | 61 | 78 | — | — | — | ? | 65 | — | — | — | — | ? | 68 | 85 | — | — | — |
| 88 | ? | 73 | — | — | — | — | ? | — | — | — | — | — | ? | 64 | 84 | — | — | — |
| 89 | 25 | 57 | 77 | — | — | — | 29 | 53 | 83 | — | — | — | ? | 62 | 82 | — | — | — |
| 91 | — | — | — | — | — | — | ? | 59 | 77 | — | — | — | ? | 61 | 82 | — | — | — |
| 92 | — | — | — | — | — | — | 28 | 67 | 84 | — | — | — | 28 | — | — | — | — | — |
| 93 | 28 | — | — | — | — | — | ? | 62 | 87 | — | — | — | ? | 64 | 84 | — | — | — |
| 94 | ? | ? | 92 | — | — | — | ? | 65 | 84 | — | — | — | ? | 69 | 89 | — | — | — |
| 95 | ? | ? | 81 | — | — | — | ? | 57 | 82 | — | — | — | ? | 64 | 84 | — | — | — |
| 96 | ? | 64 | 83 | — | — | — | 29 | 57 | 82 | — | — | — | ? | 64 | 84 | — | — | — |
| 97 | ? | 59 | 83 | — | — | — | ? | — | — | — | — | — | ? | ? | — | — | — | — |
| 98 | ? | 61 | 77 | — | — | — | ? | — | — | ? | 77 | 99 | ? | 69 | 84 | — | — | — |
| 99 | ? | 61 | 77 | — | — | — | ? | 56 | 80 | — | — | — | ? | 65 | — | — | — | — |
| 100 | 25 | 57 | 78 | — | — | — | ? | 65 | 85 | — | — | — | ? | — | — | — | — | — |
| 101 | ? | — | — | — | — | — | 32 | 62 | 79 | — | — | — | — | — | — | — | — | — |
| 102 | ? | 61 | 81 | — | — | — | ? | 53 | 79 | — | — | — | ? | 68 | 85 | — | — | — |
| 103 | 24 | 55 | 77 | — | — | — | 22 | — | — | — | — | — | ? | 72 | 89 | — | — | — |
| 104 | — | — | — | — | — | — | ? | — | — | ? | 74 | — | 37 | 68 | 89 | — | — | — |
| 105 | — | — | — | — | — | — | ? | ? | – | — | — | — | ? | 69 | 84 | — | — | — |
| 106 | — | — | — | — | — | — | 35 | — | — | — | — | — | — | — | — | — | — | — |
| 109 | — | — | — | — | — | — | ? | 56 | 77 | — | — | — | ? | 61 | 78 | — | — | — |
| 110 | — | — | — | — | — | — | 46 | 79 | — | — | — | — | ? | 70 | 92 | — | — | — |
| 111 | ? | 67 | 87 | — | — | — | ? | — | — | — | — | — | ? | 72 | 91 | — | — | — |
| 113 | — | — | — | — | — | — | ? | ? | 84 | — | — | — | 37 | — | — | — | — | — |
| 115 | ? | 73 | — | — | — | — | ? | 63 | 82 | — | — | — | ? | 70 | ? | — | — | — |
| 116 | — | — | — | — | — | — | ? | 63 | 84 | — | — | — | ? | 73 | 90 | — | — | — |
| 117 | — | — | — | — | — | — | ? | ? | 87 | — | — | — | ? | 61 | 83 | — | — | — |
| 118 | — | — | — | — | — | — | ? | ? | 84 | — | — | — | ? | 68 | 88 | — | — | — |
| 119 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | 62 | 82 | — | — | — |
| 120 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 122 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | 65 | 84 | — | — | — |
| 123 | 28 | — | — | — | — | — | ? | 58 | 79 | — | — | — | 39 | 72 | 89 | — | — | — |

**Appendix 9** (cont'd)

| Site no. | 1975 | | | | | | 1976 | | | | | | 1977 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | First egg | | | Relay | | | First egg | | | Relay | | | First egg | | | Relay | | |
| | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F |
| 124 | 26 | 59 | 77 | — | — | — | ? | 56 | ? | — | — | — | ? | — | — | — | — | — |
| 126 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 127 | 26 | 61 | 78 | — | — | — | ? | 88 | — | — | — | — | 27 | — | — | ? | — | — |
| 129 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 130 | — | — | — | — | — | — | ? | ? | — | — | — | — | — | — | — | — | — | — |
| 131 | — | — | — | — | — | — | ? | ? | — | — | — | — | — | — | — | — | — | — |
| 132 | ? | 64 | ? | — | — | — | — | — | — | — | — | — | ? | 71 | 93 | — | — | — |
| 133 | ? | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 140 | — | — | — | — | — | — | — | — | — | — | — | — | ? | — | — | — | — | — |
| 143 | — | — | — | — | — | — | — | — | — | — | — | — | 42 | 83 | ? | — | — | — |
| 145 | — | — | — | — | — | — | — | — | — | — | — | — | ? | — | — | — | — | — |
| 148 | — | — | — | — | — | — | — | — | — | — | — | — | ? | — | — | — | — | — |
| 149 | — | — | — | — | — | — | — | — | — | — | — | — | ? | — | — | — | — | — |
| Plot Q4: | | | | | | | | | | | | | | | | | | |
| 1 | — | — | — | — | — | — | 28 | 57 | 81 | — | — | — | ? | 64 | 84 | — | — | — |
| 2 | — | — | — | — | — | — | 23 | 57 | — | — | — | — | ? | 60 | 82 | — | — | — |
| 3 | — | — | — | — | — | — | — | — | — | — | — | — | ? | — | — | — | — | — |
| 4 | — | — | — | — | — | — | 23 | — | — | 55 | — | — | ? | — | — | — | — | — |
| 5 | — | — | — | — | — | — | ? | 57 | 77 | — | — | — | ? | 60 | 82 | — | — | — |
| 6 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | 65 | 88 | — | — | — |
| 7 | — | — | — | — | — | — | ? | 54 | 83 | — | — | — | 35 | 67 | 89 | — | — | — |
| 8 | — | — | — | — | — | — | ? | 65 | 83 | — | — | — | 35 | — | — | 51 | 73 | 91 |
| 9 | — | — | — | — | — | — | 26 | 57 | 82 | — | — | — | ? | 64 | 88 | — | — | — |
| 10 | — | — | — | — | — | — | ? | 67 | 84 | — | — | — | ? | 65 | 84 | — | — | — |
| 11 | — | — | — | — | — | — | 24 | 57 | 79 | — | — | — | ? | — | — | — | — | — |
| 12 | — | — | — | — | — | — | ? | 65 | 87 | — | — | — | ? | — | — | — | — | — |
| 13 | — | — | — | — | — | — | ? | 63 | 82 | — | — | — | ? | 64 | 85 | — | — | — |
| 14 | — | — | — | — | — | — | ? | ? | 82 | — | — | — | ? | 66 | 88 | — | — | — |
| 15 | — | — | — | — | — | — | ? | 67 | 84 | — | — | — | ? | 64 | 84 | — | — | — |
| 18 | — | — | — | — | — | — | 27 | ? | 82 | — | — | — | ? | 65 | 84 | — | — | — |
| 19 | — | — | — | — | — | — | 27 | 69 | — | — | — | — | ? | 64 | 84 | — | — | — |
| 20 | — | — | — | — | — | — | ? | 57 | 79 | — | — | — | ? | 62 | — | — | — | — |
| 21 | — | — | — | — | — | — | 25 | 56 | 84 | — | — | — | ? | 66 | 86 | — | — | — |
| 22 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | — | — | — | — | — |
| 23 | — | — | — | — | — | — | — | — | — | — | — | — | ? | 64 | — | — | — | — |
| 24 | — | — | — | — | — | — | 1 | 72 | — | — | — | — | ? | 64 | 84 | — | — | — |
| 25 | — | — | — | — | — | — | 22 | — | — | 45 | — | — | 44 | — | — | — | — | — |
| 26 | — | — | — | — | — | — | ? | ? | 79 | — | — | — | ? | 58 | 81 | — | — | — |
| 27 | — | — | — | — | — | — | ? | 56 | 78 | — | — | — | ? | 57 | 81 | — | — | — |
| 28 | — | — | — | — | — | — | ? | 52 | 74 | — | — | — | ? | 58 | 78 | — | — | — |
| 29 | — | — | — | — | — | — | ? | 67 | 85 | — | — | — | 24 | 59 | 82 | — | — | — |
| 30 | — | — | — | — | — | — | 26 | 54 | 79 | — | — | — | ? | 57 | 82 | — | — | — |
| 31 | — | — | — | — | — | — | ? | ? | 84 | — | — | — | ? | 60 | 84 | — | — | — |
| 32 | — | — | — | — | — | — | 25 | 57 | 80 | — | — | — | ? | 64 | 84 | — | — | — |
| 33 | — | — | — | — | — | — | 32 | 69 | — | — | — | — | ? | 60 | 82 | — | — | — |
| 34 | — | — | — | — | — | — | ? | 56 | 79 | — | — | — | ? | 64 | 84 | — | — | — |
| 35 | — | — | — | — | — | — | ? | 56 | 81 | — | — | — | ? | 60 | 84 | — | — | — |
| 36 | — | — | — | — | — | — | ? | 56 | 77 | — | — | — | ? | 64 | 84 | — | — | — |
| 37 | — | — | — | — | — | — | ? | 69 | — | — | — | — | ? | 67 | 84 | — | — | — |
| 38 | — | — | — | — | — | — | ? | 56 | 79 | — | — | — | 28 | 59 | 82 | — | — | — |
| 39 | — | — | — | — | — | — | ? | 72 | 89 | — | — | — | ? | 61 | 84 | — | — | — |
| 40 | — | — | — | — | — | — | ? | ? | 83 | — | — | — | ? | 59 | 82 | — | — | — |
| 41 | — | — | — | — | — | — | ? | 72 | — | — | — | — | 28 | 59 | 82 | — | — | — |
| 42 | — | — | — | — | — | — | 22 | 56 | 77 | — | — | — | ? | — | — | — | — | — |
| 43 | — | — | — | — | — | — | 26 | — | — | — | — | — | 44 | — | — | — | — | — |
| 44 | — | — | — | — | — | — | ? | ? | 79 | — | — | — | ? | 59 | 78 | — | — | — |
| 45 | — | — | — | — | — | — | ? | 56 | 74 | — | — | — | ? | 60 | 81 | — | — | — |
| 46 | — | — | — | — | — | — | ? | 57 | 77 | — | — | — | ? | 62 | 82 | — | — | — |
| 47 | — | — | — | — | — | — | ? | 57 | 77 | — | — | — | ? | 61 | 82 | — | — | — |
| 48 | — | — | — | — | — | — | 27 | 63 | — | — | — | — | 28 | 61 | 82 | — | — | — |
| 49 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | 69 | 89 | — | — | — |

**Appendix 9** (cont'd)

| Site no. | 1975 | | | | | | 1976 | | | | | | 1977 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | First egg | | | Relay | | | First egg | | | Relay | | | First egg | | | Relay | | |
| | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F |
| 50 | — | — | — | — | — | — | ? | 56 | 77 | — | — | — | ? | 61 | 84 | — | — | — |
| 51 | — | — | — | — | — | — | 26 | ? | 79* | — | — | — | 35 | 68 | 88 | — | — | — |
| 52 | — | — | — | — | — | — | ? | 67 | — | — | — | — | ? | — | — | — | — | — |
| 53 | — | — | — | — | — | — | ? | ? | — | — | — | — | ? | — | — | — | — | — |
| 54 | — | — | — | — | — | — | ? | ? | 82 | — | — | — | ? | 62 | 84 | — | — | — |
| 55 | — | — | — | — | — | — | 23 | ? | 79 | — | — | — | ? | 71 | 88 | — | — | — |
| 57 | — | — | — | — | — | — | 29 | ? | 88 | — | — | — | ? | 64 | 85 | — | — | — |
| 58 | — | — | — | — | — | — | 29 | — | — | 46 | 81 | — | ? | 66 | 85 | — | — | — |
| 59 | — | — | — | — | — | — | ? | 54 | 78 | — | — | — | ? | — | — | — | — | — |
| 60 | — | — | — | — | — | — | ? | ? | 79 | — | — | — | ? | 62 | 84 | — | — | — |
| 61 | — | — | — | — | — | — | ? | 57 | 77 | — | — | — | ? | 61 | 82 | — | — | — |
| 62 | — | — | — | — | — | — | 23 | 54 | 77 | — | — | — | ? | 77 | 93 | — | — | — |
| 63 | — | — | — | — | — | — | ? | 52 | 77 | — | — | — | ? | 56 | 78 | — | — | — |
| 64 | — | — | — | — | — | — | ? | 57 | 83 | — | — | — | 36 | 66 | 84 | — | — | — |
| 66 | — | — | — | — | — | — | 37 | 67 | — | — | — | — | 31 | — | — | — | — | — |
| 67 | — | — | — | — | — | — | 27 | 67 | — | — | — | — | ? | — | — | — | — | — |
| 68 | — | — | — | — | — | — | ? | 55 | 81 | — | — | — | 36 | 66 | 84 | — | — | — |
| 69 | — | — | — | — | — | — | ? | 56 | 74 | — | — | — | ? | 60 | 82 | — | — | — |
| 70 | — | — | — | — | — | — | ? | ? | — | — | — | — | ? | 58 | 78 | — | — | — |
| 72 | — | — | — | — | — | — | ? | 56 | 78 | — | — | — | 37 | 76 | 93 | — | — | — |
| 73 | — | — | — | — | — | — | ? | 63 | — | — | — | — | ? | 65 | 84 | — | — | — |
| 74 | — | — | — | — | — | — | ? | 56 | 81 | — | — | — | ? | — | — | ? | ? | 95 |
| 75 | — | — | — | — | — | — | ? | 57 | 79 | — | — | — | ? | 64 | 84 | — | — | — |
| 76 | — | — | — | — | — | — | ? | 56 | 82 | — | — | — | ? | — | — | — | — | — |
| 77 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | 60 | 79 | — | — | — |
| 78 | — | — | — | — | — | — | 23 | 56 | 75 | — | — | — | ? | — | — | ? | 81 | 99 |
| 79 | — | — | — | — | — | — | ? | 56 | 81 | — | — | — | — | — | — | — | — | — |
| 80 | — | — | — | — | — | — | ? | 56 | 77 | — | — | — | 26 | — | — | 44 | — | — |
| 81 | — | — | — | — | — | — | ? | 57 | 82 | — | — | — | ? | 62 | 82 | — | — | — |
| 82 | — | — | — | — | — | — | 41 | 72 | 91 | — | — | — | ? | 66 | 88 | — | — | — |
| 83 | — | — | — | — | — | — | ? | 56 | 77 | — | — | — | ? | 73 | 90 | — | — | — |
| 84 | — | — | — | — | — | — | 28 | 74 | — | — | — | — | ? | 64 | 84 | — | — | — |
| 85 | — | — | — | — | — | — | 38 | — | — | — | — | — | — | — | — | — | — | — |
| 86 | — | — | — | — | — | — | — | — | — | — | — | — | ? | 62 | 82 | — | — | — |
| 87 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | 65 | 85 | — | — | — |
| 88 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 89 | — | — | — | — | — | — | ? | — | — | 50 | — | — | ? | 66 | 91 | — | — | — |
| 90 | — | — | — | — | — | — | ? | — | — | — | — | — | ? | — | — | ? | ? | 94 |
| 91 | — | — | — | — | — | — | ? | 69 | — | — | — | — | — | — | — | — | — | — |
| 92 | — | — | — | — | — | — | ? | 67 | 84 | — | — | — | ? | 64 | — | — | — | — |
| 93 | — | — | — | — | — | — | ? | 63 | 79 | — | — | — | ? | — | — | — | — | — |
| 94 | — | — | — | — | — | — | ? | 54 | 78 | — | — | — | ? | 64 | 84 | — | — | — |
| 95 | — | — | — | — | — | — | ? | 67 | 84 | — | — | — | 36 | 68 | 89 | — | — | — |
| 96 | — | — | — | — | — | — | ? | — | — | — | — | — | 42 | 74 | — | — | — | — |
| 97 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| Plot S1: | | | | | | | | | | | | | | | | | | |
| 1 | ? | 71 | ? | — | — | — | ? | 65 | 93 | — | — | — | 38 | 71 | 89 | — | — | — |
| 2 | 27 | 60 | 84 | — | — | — | 27 | 63 | 83 | — | — | — | 30 | 61 | 83 | — | — | — |
| 3 | 31 | ? | 91 | — | — | — | 27 | 60 | 83 | — | — | — | 32 | 65 | 86 | — | — | — |
| 4 | ? | ? | ? | — | — | — | ? | 56 | 79 | — | — | — | 34 | 63 | 83 | — | — | — |
| 5 | ? | 64 | 84 | — | — | — | 28 | — | — | — | — | — | ? | — | — | — | — | — |
| 6 | 31 | 67 | 87 | — | — | — | ? | 64 | 81 | — | — | — | 44 | 76 | — | — | — | — |
| 7 | ? | ? | 79 | — | — | — | ? | 58 | 77 | — | — | — | 27 | 56 | 75 | — | — | — |
| 8 | ? | 64 | 83 | — | — | — | ? | 56 | 76 | — | — | — | ? | 59 | 79 | — | — | — |
| 9 | 26 | 58 | 82 | — | — | — | 22 | 56 | 76 | — | — | — | 33 | 65 | 84 | — | — | — |
| 10 | 31 | 63 | 79 | — | — | — | ? | 59 | 81 | — | — | — | ? | — | — | — | — | — |
| 11 | 27 | 58 | 77 | — | — | — | 23 | 53 | 79 | — | — | — | ? | — | — | — | — | — |
| 12 | ? | 56 | 75 | — | — | — | ? | 53 | 76 | — | — | — | ? | 60 | — | — | — | — |
| 13 | 27 | 57 | 78 | — | — | — | 23 | 56 | 76 | — | — | — | 25 | 57 | 78 | — | — | — |
| 14 | ? | 71 | 87 | — | — | — | — | — | — | — | — | — | ? | 60 | 82 | — | — | — |
| 15 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 16 | 29 | 61 | 84 | — | — | — | 24 | 59 | 80 | — | — | — | 48 | 81 | 99 | — | — | — |

**Appendix 9** (cont'd)

| Site no. | 1975 | | | | | | 1976 | | | | | | 1977 | | | | | |
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| | First egg | | | Relay | | | First egg | | | Relay | | | First egg | | | Relay | | |
| | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F |
| 17 | ? | — | — | — | — | — | 33 | — | — | — | — | — | ? | — | — | — | — | — |
| 18 | ? | 58 | 77 | — | — | — | 22 | 54 | 79 | — | — | — | 22 | 56 | 79 | — | — | — |
| 19 | 30 | 60 | 79 | — | — | — | 27 | — | — | — | — | — | 34 | — | — | — | — | — |
| 20 | 26 | 58 | 77 | — | — | — | 22 | 52 | 79 | — | — | — | 31 | 64 | 83 | — | — | — |
| 21 | ? | 61 | 84 | — | — | — | 33 | 61 | 79 | — | — | — | 32 | 63 | 83 | — | — | — |
| 22 | 29 | 61 | 84 | — | — | — | 27 | 61 | 86 | — | — | — | ? | 65 | — | — | — | — |
| 23 | 24 | — | — | ? | 63 | 90 | 26 | 61 | 81 | — | — | — | ? | 65 | 85 | — | — | — |
| 24 | 27 | 58 | 82 | — | — | — | 30 | 60 | 81 | — | — | — | ? | 59 | 84 | — | — | — |
| 25 | 27 | 60 | 82 | — | — | — | 31 | 62 | 86 | — | — | — | 27 | 59 | 83 | — | — | — |
| 26 | 30 | 60 | 83 | — | — | — | 25 | — | — | — | — | — | ? | 62 | 84 | — | — | — |
| 27 | 29 | 60 | 79 | — | — | — | 25 | 57 | 79 | — | — | — | ? | — | — | — | — | — |
| 28 | 28 | 60 | 79 | — | — | — | ? | 59 | 81 | — | — | — | 40 | 72 | 91 | — | — | — |
| 29 | 25 | 58 | — | — | — | — | 32 | 64 | 82 | — | — | — | 33 | — | — | — | — | — |
| 30 | 35 | — | — | — | — | — | 37 | 62 | 83 | — | — | — | 35 | 68 | 89 | — | — | — |
| 31 | ? | 67 | 91 | — | — | — | 42 | 73 | 93 | — | — | — | 35 | 69 | 91 | — | — | — |
| 32 | 24 | 55 | 77 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 33 | 27 | 56 | 76 | — | — | — | 28 | 58 | 81 | — | — | — | 42 | — | — | — | — | — |
| 34 | 29 | 61 | 83 | — | — | — | 34 | 66 | 87 | — | — | — | ? | 63 | 84 | — | — | — |
| 35 | 30 | 61 | 85 | — | — | — | — | — | — | — | — | — | ? | 69 | 89 | — | — | — |
| 36 | 25 | 57 | 78 | — | — | — | 32 | 55 | 74 | — | — | — | ? | 56 | 74 | — | — | — |
| 37 | 29 | 60 | 79 | — | — | — | ? | ? | — | — | — | — | ? | 75 | 93 | — | — | — |
| 38 | 25 | — | — | — | — | — | 24 | 56 | 77 | — | — | — | 26 | 57 | 78 | — | — | — |
| 39 | ? | 64 | 90 | — | — | — | ? | 56 | 77 | — | — | — | ? | 59 | 75 | — | — | — |
| 40 | 30 | 62 | 82 | — | — | — | 28 | 59 | 78 | — | — | — | 32 | 62 | 83 | — | — | — |
| 41 | ? | 73 | 91 | — | — | — | ? | 63 | 78 | — | — | — | 33 | — | — | — | — | — |
| 42 | ? | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 43 | ? | 55 | 73 | — | — | — | ? | 53 | 74 | — | — | — | 22 | 54 | 75 | — | — | — |
| 44 | 36 | ? | 92 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 45 | 25 | — | — | — | — | — | — | — | — | — | — | — | 48 | — | — | — | — | — |
| 46 | 29 | 61 | 85 | — | — | — | 27 | 60 | — | — | — | — | 34 | 66 | 87 | — | — | — |
| 47 | ? | 61 | 78 | — | — | — | 42 | 75 | — | — | — | — | 34 | — | — | — | — | — |
| 48 | ? | 57 | 78 | — | — | — | ? | 53 | 79 | — | — | — | ? | — | — | — | — | — |
| 49 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 50 | 35 | — | — | 52 | — | — | 33 | — | — | — | — | — | — | — | — | — | — | — |
| 51 | 27 | 60 | 82 | — | — | — | ? | 59 | 79 | — | — | — | ? | 65 | 85 | — | — | — |
| 52 | ? | 61 | 89 | — | — | — | 27 | 61 | 79 | — | — | — | — | — | — | — | — | — |
| 53 | 29 | — | — | — | — | — | 20 | — | — | 38 | 69 | 89 | 29 | 62 | 83 | — | — | — |
| 54 | ? | 62 | 83 | — | — | — | ? | 59 | 79 | — | — | — | ? | 72 | 94 | — | — | — |
| 55 | ? | 57 | 79 | — | — | — | ? | 55 | 74 | — | — | — | ? | 57 | 80 | — | — | — |
| 56 | 31 | 60 | 87 | — | — | — | ? | 61 | 84 | — | — | — | 31 | 66 | 85 | — | — | — |
| 57 | 37 | 60 | 79 | — | — | — | ? | 57 | 84 | — | — | — | — | — | — | — | — | — |
| 58 | 30 | 61 | — | — | — | — | 27 | 63 | 87 | — | — | — | ? | 82 | 99 | — | — | — |
| 59 | 27 | 60 | 83 | — | — | — | 33 | — | — | — | — | — | ? | 67 | 87 | — | — | — |
| 60 | 30 | — | — | — | — | — | ? | 63 | 79 | — | — | — | ? | 70 | 84 | — | — | — |
| 61 | 47 | 78 | — | — | — | — | 24 | 61 | 86 | — | — | — | ? | 65 | 84 | — | — | — |
| 63 | 25 | 57 | 77 | — | — | — | ? | 55 | 76 | — | — | — | ? | 56 | 75 | — | — | — |
| 64 | ? | 60 | 79 | — | — | — | 27 | 61 | 77 | — | — | — | 24 | — | — | — | — | — |
| 65 | 27 | 60 | 79 | — | — | — | ? | 57 | 79 | — | — | — | 23 | 55 | 75 | — | — | — |
| 66 | 29 | 61 | — | — | — | — | ? | — | — | 43 | 76 | 94 | 29 | 61 | 82 | — | — | — |
| 67 | 31 | 64 | 85 | — | — | — | ? | 61 | 79 | — | — | — | ? | 62 | 79 | — | — | — |
| 68 | ? | 58 | 77 | — | — | — | ? | 54 | 74 | — | — | — | ? | 62 | 82 | — | — | — |
| 69 | 24 | 57 | 78 | — | — | — | 24 | 57 | 81 | — | — | — | 25 | 58 | 82 | — | — | — |
| 70 | ? | 66 | 92 | — | — | — | 34 | 64 | 87 | — | — | — | ? | 65 | 85 | — | — | — |
| 71 | ? | 56 | 76 | — | — | — | ? | 66 | 88 | — | — | — | ? | 57 | 79 | — | — | — |
| 73 | 28 | 61 | 84 | — | — | — | ? | ? | 85 | — | — | — | 33 | 64 | 83 | — | — | — |
| 74 | 27 | — | — | — | — | — | 29 | 61 | 84 | — | — | — | 30 | 63 | 84 | — | — | — |
| 75 | ? | 61 | 84 | — | — | — | — | — | — | — | — | — | ? | 69 | 89 | — | — | — |
| 76 | 30 | 60 | 87 | — | — | — | 25 | 58 | 81 | — | — | — | ? | 63 | 84 | — | — | — |
| 77 | 31 | — | — | — | — | — | 26 | 58 | 87 | — | — | — | ? | 68 | 84 | — | — | — |
| 78 | ? | 55 | 73 | — | — | — | 23 | 56 | 73 | — | — | — | ? | — | — | 42 | 74 | 94 |
| 79 | — | — | — | — | — | — | — | — | — | — | — | — | 34 | 65 | 87 | — | — | — |
| 80 | ? | 62 | 87 | — | — | — | ? | 59 | 85 | — | — | — | 34 | 66 | 85 | — | — | — |
| 81 | 24 | 56 | 78 | — | — | — | ? | 58 | 78 | — | — | — | ? | 57 | — | — | — | — |

**Appendix 9** (cont'd)

| Site no. | 1975 | | | | | | 1976 | | | | | | 1977 | | | | | |
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| | First egg | | | Relay | | | First egg | | | Relay | | | First egg | | | Relay | | |
| | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F |
| 82 | 26 | 58 | 82 | — | — | — | ? | 62 | 82 | — | — | — | ? | 61 | 84 | — | — | — |
| 83 | 28 | 60 | 84 | — | — | — | 41 | 73 | 95 | — | — | — | 33 | — | — | — | — | — |
| 84 | 34 | 65 | 87 | — | — | — | 27 | — | — | — | — | — | 30 | 67 | 85 | — | — | — |
| 85 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 86 | 29 | — | — | — | — | — | ? | — | — | — | — | — | 35 | — | — | — | — | — |
| 87 | 25 | 56 | 79 | — | — | — | ? | 66 | 87 | — | — | — | ? | 76 | 94 | — | — | — |
| 88 | 29 | 62 | 80 | — | — | — | ? | 62 | 87 | — | — | — | ? | 68 | 85 | — | — | — |
| 89 | 31 | 64 | 87 | — | — | — | 45 | 81 | — | — | — | — | 36 | 69 | 87 | — | — | — |
| 90 | 41 | 71 | — | — | — | — | 35 | 65 | 88 | — | — | — | 32 | 64 | 89 | — | — | — |
| 91 | 29 | 60 | 84 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 92 | ? | 63 | 85 | — | — | — | ? | — | — | 43 | — | — | ? | 80 | 99 | — | — | — |
| 93 | — | — | — | — | — | — | 24 | — | — | — | — | — | 29 | 63 | 82 | — | — | — |
| 94 | 35 | — | — | ? | — | — | 28 | 61 | 81 | — | — | — | ? | 67 | 88 | — | — | — |
| 95 | ? | — | — | — | — | — | 34 | 71 | 87 | — | — | — | 42 | — | — | — | — | — |
| 96 | 31 | 66 | 87 | — | — | — | 27 | 59 | 81 | — | — | — | 40 | 72 | 93 | — | — | — |
| 97 | 38 | — | — | — | — | — | 23 | — | — | — | — | — | 27 | — | — | 49 | 79 | 98 |
| 98 | 28 | 60 | 82 | — | — | — | ? | 61 | 82 | — | — | — | 41 | 73 | 92 | — | — | — |
| 100 | 30 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 101 | 29 | — | — | ? | 83 | — | ? | 58 | 78 | — | — | — | 43 | 75 | 94 | — | — | — |
| 102 | 26 | 58 | 79 | — | — | — | 24 | — | — | — | — | — | 34 | 62 | 84 | — | — | — |
| 103 | ? | 62 | 87 | — | — | — | 28 | 60 | 78 | — | — | — | ? | — | — | — | — | — |
| 104 | ? | 64 | 87 | — | — | — | 34 | 66 | 87 | — | — | — | 34 | 66 | 88 | — | — | — |
| 105 | 27 | 60 | 82 | — | — | — | ? | 57 | 78 | — | — | — | 35 | 66 | 84 | — | — | — |
| 107 | 31 | 60 | 79 | — | — | — | 34 | 57 | 89 | — | — | — | 31 | 63 | 84 | — | — | — |
| 108 | 31 | — | — | — | — | — | 34 | — | — | — | — | — | 40 | 69 | 93 | — | — | — |
| 109 | 30 | 62 | 87 | — | — | — | ? | 71 | 90 | — | — | — | ? | 64 | 84 | — | — | — |
| 110 | 28 | 60 | 78 | — | — | — | 42 | 73 | 91 | — | — | — | 28 | 60 | 79 | — | — | — |
| 111 | 28 | 60 | 79 | — | — | — | ? | 72 | 91 | — | — | — | 26 | — | — | — | — | — |
| 113 | 30 | 60 | 82 | — | — | — | 45 | 75 | 94 | — | — | — | ? | 59 | 82 | — | — | — |
| 114 | 29 | 61 | 79 | — | — | — | ? | — | — | ? | 76 | 94 | 34 | 64 | 84 | — | — | — |
| 115 | 25 | 57 | 78 | — | — | — | ? | — | — | 44 | 75 | 94 | 26 | — | — | — | — | — |
| 116 | 24 | 58 | 77 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 117 | 29 | 60 | 79 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 118 | ? | 69 | 90 | — | — | — | — | — | — | — | — | — | 42 | 74 | 93 | — | — | — |
| 119 | ? | 63 | 84 | — | — | — | 44 | 75 | 93 | — | — | — | 34 | 69 | 85 | — | — | — |
| 120 | 41 | — | — | — | — | — | — | — | — | — | — | 66 | — | — | — | — | — | — |
| 121 | ? | 61 | 79 | — | — | — | 31 | — | — | ? | — | — | 33 | 64 | 84 | — | — | — |
| 122 | ? | 61 | 82 | — | — | — | ? | 58 | 79 | — | — | — | ? | 64 | 85 | — | — | — |
| 123 | 27 | 58 | 78 | — | — | — | 42 | 71 | 90 | — | — | — | 28 | 62 | 82 | — | — | — |
| 124 | 31 | 61 | 85 | — | — | — | ? | — | — | 42 | 73 | 91 | 28 | 60 | 82 | — | — | — |
| 125 | ? | 73 | 91 | — | — | — | 42 | 65 | 84 | — | — | — | 31 | 76 | — | — | — | — |
| 126 | 31 | 63 | 82 | — | — | — | 42 | — | — | — | — | — | ? | 69 | 89 | — | — | — |
| 127 | 31 | 60 | 79 | — | — | — | ? | 76 | 94 | — | — | — | 26 | 58 | 79 | — | — | — |
| 128 | 35 | ? | 85 | — | — | — | 45 | 76 | 93 | — | — | — | ? | 65 | 88 | — | — | — |
| 129 | 30 | 61 | 83 | — | — | — | ? | 67 | 91 | — | — | — | ? | 67 | 89 | — | — | — |
| 130 | ? | — | — | ? | 83 | — | ? | — | — | ? | 73 | 93 | ? | 65 | 84 | — | — | — |
| 131 | 27 | 60 | 79 | — | — | — | 22 | 56 | 79 | — | — | — | 28 | 62 | 82 | — | — | — |
| 132 | 27 | 60 | 82 | — | — | — | 38 | 70 | 89 | — | — | — | 29 | 62 | 82 | — | — | — |
| 133 | 27 | — | — | — | — | — | 27 | 58 | 79 | — | — | — | 29 | 63 | 84 | — | — | — |
| 134 | 29 | 62 | 84 | — | — | — | ? | 58 | 80 | — | — | — | ? | 59 | 82 | — | — | — |
| 135 | 35 | 66 | 87 | — | — | — | ? | 58 | 80 | — | — | — | 49 | — | — | — | — | — |
| 136 | 31 | 61 | 82 | — | — | — | ? | 61 | 80 | — | — | — | 28 | 58 | 78 | — | — | — |
| 137 | 31 | 62 | 84 | — | — | — | 26 | 56 | 81 | — | — | — | — | — | — | — | — | — |
| 138 | 31 | — | — | — | — | — | ? | 61 | 84 | — | — | — | ? | 62 | 84 | — | — | — |
| 139 | 31 | 60 | 84 | — | — | — | ? | 64 | 84 | — | — | — | ? | 62 | 82 | — | — | — |
| 140 | 28 | 60 | 84 | — | — | — | ? | 62 | 87 | — | — | — | 33 | 63 | 84 | — | — | — |
| 141 | 29 | — | — | 46 | 79 | ? | ? | 63 | 84 | — | — | — | 35 | 67 | 85 | — | — | — |
| 142 | ? | — | — | — | — | — | 33 | 66 | 86 | — | — | — | 34 | — | — | — | — | — |
| 143 | 30 | 61 | 84 | — | — | — | ? | 76 | 93 | — | — | — | ? | 69 | 88 | — | — | — |
| 144 | 31 | — | — | — | — | — | ? | 62 | 84 | — | — | — | ? | 65 | 89 | — | — | — |
| 145 | 31 | — | — | — | — | — | ? | 62 | 84 | — | — | — | 33 | 64 | 84 | — | — | — |
| 146 | 28 | 60 | — | — | — | — | 23 | 55 | 77 | — | — | — | 28 | 60 | 79 | — | — | — |
| 147 | 29 | 60 | 87 | — | — | — | — | — | — | — | — | — | 44 | 77 | 94 | — | — | — |

**Appendix 9** (cont'd)

| Site no. | 1975 | | | | | | 1976 | | | | | | 1977 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | First egg | | | Relay | | | First egg | | | Relay | | | First egg | | | Relay | | |
| | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F |
| 148 | 42 | 73 | 91 | — | — | — | — | — | — | — | — | — | ? | 65 | 86 | — | — | — |
| 149 | ? | 61 | 84 | — | — | — | ? | — | — | — | — | — | ? | — | — | — | — | — |
| 150 | ? | 60 | 79 | — | — | — | ? | 79 | 99 | — | — | — | ? | 61 | 84 | — | — | — |
| 151 | 35 | — | — | — | — | — | ? | 80 | 97 | — | — | — | 38 | 70 | — | — | — | — |
| 152 | 31 | 64 | 87 | — | — | — | — | — | — | — | — | — | ? | 64 | 84 | — | — | — |
| 153 | ? | 58 | 82 | — | — | — | — | — | — | — | — | — | 31 | — | — | 45 | 77 | 96 |
| 154 | ? | 58 | 77 | — | — | — | ? | 61 | 79 | — | — | — | ? | 58 | 79 | — | — | — |
| 155 | 46 | — | — | — | — | — | — | — | — | — | — | — | 39 | 72 | 92 | — | — | — |
| 156 | 28 | 61 | 78 | — | — | — | 27 | 61 | 81 | — | — | — | 28 | 61 | 84 | — | — | — |
| 157 | 30 | 63 | — | — | — | — | 36 | — | — | — | — | — | 31 | — | — | — | — | — |
| 158 | ? | 60 | 82 | — | — | — | 30 | 61 | 83 | — | — | — | ? | 61 | 85 | — | — | — |
| 159 | 34 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 160 | 31 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 161 | 29 | 61 | 83 | — | — | — | ? | — | — | 47 | 80 | — | — | — | — | — | — | — |
| 162 | 30 | 62 | 82 | — | — | — | 42 | — | — | — | — | — | 51 | 82 | 98 | — | — | — |
| 163 | 34 | 67 | 88 | — | — | — | — | — | — | — | — | — | 35 | — | — | 52 | 84 | 100 |
| 164 | ? | 62 | 82 | — | — | — | — | — | — | — | — | — | 36 | 67 | 84 | — | — | — |
| 165 | ? | 62 | 85 | — | — | — | ? | 80 | — | — | — | — | ? | 80 | 96 | — | — | — |
| 166 | ? | — | — | — | — | — | 37 | 64 | 87 | — | — | — | 35 | 68 | 85 | — | — | — |
| 167 | 26 | 58 | 77 | — | — | — | 34 | 66 | — | — | — | — | — | — | — | 54 | — | — |
| 168 | 30 | 60 | 79 | — | — | — | 41 | 77 | 94 | — | — | — | 33 | — | — | 46 | 76 | 94 |
| 170 | ? | 63 | 83 | — | — | — | ? | — | — | — | — | — | ? | 61 | 84 | — | — | — |
| 171 | 28 | — | — | ? | 88 | — | 38 | 64 | 85 | — | — | — | 31 | 59 | 79 | — | — | — |
| 172 | — | — | — | — | — | — | ? | 65 | — | — | — | — | ? | 64 | 84 | — | — | — |
| 173 | 30 | 61 | 87 | — | — | — | ? | 59 | 82 | — | — | — | — | — | — | — | — | — |
| 174 | 36 | 66 | 88 | — | — | — | 35 | 66 | 89 | — | — | — | 40 | — | — | — | — | — |
| 175 | 31 | — | — | — | — | — | 22 | 57 | 78 | — | — | — | 29 | 62 | 84 | — | — | — |
| 176 | 24 | 55 | 73 | — | — | — | — | — | — | 45 | 55 | 78 | 22 | — | — | — | — | — |
| 177 | 26 | 58 | 77 | — | — | — | ? | 60 | 79 | — | — | — | 33 | 66 | 85 | — | — | — |
| 178 | 28 | 58 | 83 | — | — | — | ? | 56 | — | — | — | — | 31 | 61 | 83 | — | — | — |
| 179 | — | — | — | — | — | — | ? | 60 | 81 | — | — | — | 32 | 64 | 84 | — | — | — |
| 180 | ? | ? | 84 | — | — | — | ? | 58 | 84 | — | — | — | 30 | 65 | 84 | — | — | — |
| 181 | — | — | — | — | — | — | ? | 56 | 79 | — | — | — | 29 | 62 | 87 | — | — | — |
| 182 | 36 | — | — | ? | — | — | ? | ? | 94 | — | — | — | 40 | 72 | 93 | — | — | — |
| 183 | 31 | — | — | — | — | — | ? | 65 | 89 | — | — | — | 28 | 62 | 84 | — | — | — |
| 185 | — | — | — | — | — | — | ? | 80 | 96 | — | — | — | 34 | 65 | 88 | — | — | — |
| 186 | — | — | — | — | — | — | ? | 71 | 89 | — | — | — | ? | 67 | 85 | — | — | — |
| 189 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 191 | 24 | 55 | 76 | — | — | — | ? | 53 | 80 | — | — | — | ? | 55 | 75 | — | — | — |
| 195 | 34 | 67 | 88 | — | — | — | ? | 63 | 89 | — | — | — | 38 | — | — | — | — | — |
| 196 | 30 | 62 | 85 | — | — | — | ? | 61 | 85 | — | — | — | ? | 67 | 82 | — | — | — |
| 197 | 31 | ? | 84 | — | — | — | ? | — | — | ? | 66 | 87 | 32 | 65 | 84 | — | — | — |
| 198 | — | — | — | — | — | — | ? | — | — | — | — | — | 38 | — | — | — | — | — |
| 199 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 200 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 201 | — | — | — | — | — | — | ? | 58 | 79 | — | — | — | 32 | — | — | — | — | — |
| 203 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 204 | 26 | 58 | 78 | — | — | — | ? | 72 | 91 | — | — | — | 31 | — | — | 47 | 80 | 99 |
| 205 | — | — | — | — | — | — | ? | 62 | 84 | — | — | — | — | — | — | — | — | — |
| 206 | — | — | — | — | — | — | ? | 64 | 84 | — | — | — | — | — | — | — | — | — |
| 207 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 208 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 211 | — | — | — | — | — | — | ? | 83 | — | — | — | — | ? | — | — | — | — | — |
| 212 | ? | 64 | 83 | — | — | — | ? | 68 | 86 | — | — | — | 32 | 64 | 84 | — | — | — |
| 213 | ? | 60 | 84 | — | — | — | ? | 61 | 79 | — | — | — | 33 | 65 | 84 | — | — | — |
| 214 | — | — | — | — | — | — | ? | 61 | 79 | — | — | — | ? | 66 | 84 | — | — | — |
| 215 | — | — | — | — | — | — | ? | 81 | — | — | — | — | 40 | 72 | 91 | — | — | — |
| 216 | — | — | — | — | — | — | ? | 69 | 93 | — | — | — | — | — | — | — | — | — |
| 217 | 35 | ? | 84 | — | — | — | ? | 72 | 90 | — | — | — | ? | 68 | 83 | — | — | — |
| 219 | 36 | 68 | 88 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 229 | — | — | — | — | — | — | — | — | — | — | — | — | ? | 73 | 94 | — | — | — |
| 230 | — | — | — | — | — | — | — | — | — | — | — | — | ? | 82 | 96 | — | — | — |
| 231 | — | — | — | — | — | — | — | — | — | — | — | — | ? | — | — | — | — | — |

**Appendix 9** (cont'd)

| Site | 1975 | | | | | | 1976 | | | | | | 1977 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | First egg | | | Relay | | | First egg | | | Relay | | | First egg | | | Relay | | |
| no. | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F |
| 232 | — | — | — | — | — | — | — | — | — | — | — | — | 35 | — | — | — | — | — |
| 235 | — | — | — | — | — | — | — | — | — | — | — | — | 10 | 76 | 95 | — | — | — |
| Plot U: | | | | | | | | | | | | | | | | | | |
| 1 | ? | 64 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 2 | ? | 61 | 79 | — | — | — | 31 | 63 | 84 | — | — | — | — | — | — | — | — | — |
| 3 | ? | — | — | — | — | — | 41 | — | — | — | — | — | — | — | — | — | — | — |
| 4 | ? | 73 | 92 | — | — | — | 22 | — | — | — | — | — | 38 | — | — | — | — | — |
| 5 | ? | 73 | 88 | — | — | — | 29 | 62 | 87 | — | — | — | ? | 61 | 83 | — | — | — |
| 6 | ? | 60 | 87 | — | — | — | 28 | 63 | 87 | — | — | — | 37 | 70 | 92 | — | — | — |
| 7 | ? | 57 | 77 | — | — | — | 24 | 64 | — | — | — | — | ? | — | — | — | — | — |
| 8 | ? | — | — | — | — | — | 40 | — | — | — | — | — | 30 | — | — | — | — | — |
| 9 | 27 | 60 | 78 | — | — | — | 27 | 60 | 82 | — | — | — | 29 | 61 | 79 | — | — | — |
| 10 | ? | 62 | 82 | — | — | — | 33 | 64 | 83 | — | — | — | 33 | 66 | 85 | — | — | — |
| 11 | ? | 61 | 79 | — | — | — | 24 | — | — | 40 | 69 | 89 | 33 | — | — | — | — | — |
| 12 | 26 | 58 | 79 | — | — | — | 29 | 60 | 82 | — | — | — | — | — | — | — | — | — |
| 13 | 28 | 64 | 83 | — | — | — | 31 | — | — | — | — | — | 33 | 69 | — | — | — | — |
| 14 | ? | 73 | 92 | — | — | — | 26 | 60 | 82 | — | — | — | 29 | — | — | 63 | — | — |
| 15 | ? | 60 | 82 | — | — | — | 26 | — | — | 43 | 75 | 92 | 31 | — | — | 62 | 93 | — |
| 16 | ? | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 17 | ? | 62 | 82 | — | — | — | 23 | 55 | 77 | — | — | — | 36 | 69 | 88 | — | — | — |
| 18 | 27 | 58 | 77 | — | — | — | ? | 57 | 80 | — | — | — | 26 | — | — | — | — | — |
| 19 | ? | 60 | 82 | — | — | — | ? | 61 | 79 | — | — | — | ? | 68 | 88 | — | — | — |
| 20 | ? | 60 | — | — | — | — | 26 | 60 | 82 | — | — | — | 35 | 68 | 38 | — | — | — |
| 21 | 25 | 57 | 77 | — | — | — | 26 | — | — | — | — | — | — | — | — | — | — | — |
| 22 | ? | 62 | 83 | — | — | — | 32 | 64 | 87 | — | — | — | 40 | 73 | 93 | — | — | — |
| 23 | ? | 58 | 77 | — | — | — | 32 | ? | 82 | — | — | — | — | — | — | — | — | — |
| 24 | ? | 62 | 83 | — | — | — | 32 | 60 | 82 | — | — | — | — | — | — | — | — | — |
| 25 | ? | — | — | — | — | — | 29 | 65 | 82 | — | — | — | — | — | — | — | — | — |
| 26 | 25 | 56 | 73 | — | — | — | 29 | 61 | 83 | — | — | — | — | — | — | — | — | — |
| 27 | ? | ? | 83 | — | — | — | ? | 65 | 83 | — | — | — | 35 | 67 | 85 | — | — | — |
| 28 | ? | 73 | — | — | — | — | 23 | 60 | 82 | — | — | — | ? | — | — | — | — | — |
| 29 | ? | 66 | 87 | — | — | — | 31 | — | — | — | — | — | 38 | 72 | 92 | — | — | — |
| 30 | 27 | 61 | 83 | — | — | — | 31 | 69 | 87 | — | — | — | — | — | — | — | — | — |
| 31 | 27 | 59 | 77 | — | — | — | 25 | — | — | — | — | — | — | — | — | — | — | — |
| 32 | ? | 62 | 82 | — | — | — | 31 | — | — | — | — | — | 39 | 72 | 88 | — | — | — |
| 33 | ? | 64 | 83 | — | — | — | 28 | 58 | 82 | — | — | — | 32 | 63 | 84 | — | — | — |
| 34 | 28 | 57 | 77 | — | — | — | 24 | 55 | 77 | — | — | — | 25 | 57 | 77 | — | — | — |
| 35 | 23 | 55 | 77 | — | — | — | 26 | 55 | 77 | — | — | — | 30 | 62 | 84 | — | — | — |
| 36 | ? | 55 | — | — | — | — | 26 | — | — | — | — | — | — | — | — | — | — | — |
| 37 | 23 | 55 | 73 | — | — | — | 27 | 60 | 82 | — | — | — | 31 | 63 | 84 | — | — | — |
| 38 | ? | 73 | — | — | — | — | 35 | 64 | 82 | — | — | — | 32 | — | — | — | — | — |
| 39 | 23 | 55 | 73 | — | — | — | 22 | 53 | 76 | — | — | — | 29 | 62 | 83 | — | — | — |
| 40 | 28 | 59 | 77 | — | — | — | 24 | 56 | 77 | — | — | — | 28 | 61 | — | — | — | — |
| 41 | 26 | 57 | 77 | — | — | — | 33 | 66 | 83 | — | — | — | 31 | — | — | — | — | — |
| 42 | 27 | 57 | 76 | — | — | — | 33 | 67 | 89 | — | — | — | — | — | — | — | — | — |
| 43 | ? | 57 | 78 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 44 | 29 | 62 | 79 | — | — | — | 41 | 77 | 96 | — | — | — | 36 | — | — | — | — | — |
| 45 | ? | 67 | — | — | — | — | 26 | — | — | — | — | — | 33 | 65 | 88 | — | — | — |
| 46 | 28 | 58 | 77 | — | — | — | 33 | ? | 83 | — | — | — | 35 | 65 | 85 | — | — | — |
| 47 | — | — | — | — | — | — | 32 | 63 | 87 | — | — | — | ? | 63 | 84 | — | — | — |
| 48 | 28 | — | — | ? | 73 | ? | 28 | 60 | 82 | — | — | — | 28 | 61 | 82 | — | — | — |
| 49 | 23 | 55 | 74 | — | — | — | 24 | 60 | 83 | — | — | — | 30 | 65 | 84 | — | — | — |
| 50 | 23 | 54 | 76 | — | — | — | 26 | — | — | — | — | — | 30 | 62 | 84 | — | — | — |
| 51 | 28 | 60 | 77 | — | — | — | ? | ? | — | — | — | — | — | — | — | — | — | — |
| 52 | ? | ? | 88 | — | — | — | 29 | 67 | 89 | — | — | — | — | — | — | — | — | — |
| 53 | — | — | — | — | — | — | 24 | 61 | 78 | — | — | — | ? | 67 | 84 | — | — | — |
| 55 | 23 | 55 | 76 | — | — | — | 28 | — | — | 45 | 80 | — | 26 | — | — | 43 | ? | 94 |
| 56 | ? | 57 | 77 | — | — | — | 28 | 62 | 83 | — | — | — | ? | 68 | — | — | — | — |
| 57 | ? | 67 | — | — | — | — | 28 | 60 | — | — | — | — | 36 | 67 | — | — | — | — |
| 58 | 28 | 58 | 82 | — | — | — | 24 | 60 | 82 | — | — | — | 28 | 59 | 82 | — | — | — |
| 59 | 29 | 64 | 82 | — | — | — | 30 | 61 | 82 | — | — | — | — | — | — | — | — | — |
| 60 | 29 | 64 | 81 | — | — | — | 27 | — | — | — | — | — | 31 | 62 | 82 | — | — | — |

**Appendix 9** (cont'd)

| Site no. | 1975 | | | | | | 1976 | | | | | | 1977 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | First egg | | | Relay | | | First egg | | | Relay | | | First egg | | | Relay | | |
| | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F | L | H | F |
| 61 | ? | 67 | ? | — | — | — | 31 | 62 | — | — | — | — | 36 | — | — | — | — | — |
| 62 | 28 | 60 | 77 | — | — | — | ? | 60 | 80 | — | — | — | 30 | 62 | 84 | — | — | — |
| 63 | 26 | 55 | 76 | — | — | — | ? | 56 | 77 | — | — | — | 31 | 65 | 83 | — | — | — |
| 66 | ? | 64 | 64 | — | — | — | ? | 61 | 85 | — | — | — | 31 | 63 | 99 | — | — | — |
| 67 | — | — | — | — | — | — | ? | 70 | 89 | — | — | — | — | — | — | — | — | — |
| 68 | — | — | — | — | — | — | ? | — | — | — | — | — | 34 | — | — | — | — | — |
| 69 | — | — | — | — | — | — | ? | — | — | — | — | — | — | — | — | — | — | — |
| 71 | ? | 77 | ? | — | — | — | ? | 61 | 85 | — | — | — | 32 | 64 | 88 | — | — | — |
| 72 | — | — | — | — | — | — | ? | 68 | 87 | — | — | — | ? | 66 | 85 | — | — | — |
| 73 | — | — | — | — | — | — | — | — | — | — | — | — | 40 | — | — | — | — | — |
| 74 | 28 | 61 | 79 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 75 | 29 | 62 | 87 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 76 | ? | 62 | 82 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 77 | ? | 61 | 82 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 78 | ? | 67 | 87 | — | — | — | — | — | — | — | — | — | 43 | 77 | 93 | — | — | — |
| 79 | ? | — | — | — | — | — | — | — | — | — | — | — | 42 | 74 | 93 | — | — | — |

* Dash indicates no data. ? indicates an unknown date.

**Appendix 10**
Dates of laying of first eggs known within 48 h at seven study plots in 1976

| Date of egg laying | Study plot | | | | | | | Totals |
|---|---|---|---|---|---|---|---|---|
| | G1 | G4 | N | Q1 | Q4 | S1 | U | |
| 20 June | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 |
| 21 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 4 |
| 22 | 2 | 3 | 0 | 7 | 2 | 5 | 2 | 21 |
| 23 | 4 | 3 | 1 | 0 | 5 | 5 | 2 | 20 |
| 24 | 0 | 2 | 1 | 0 | 1 | 6 | 7 | 17 |
| 25 | 2 | 1 | 4 | 3 | 2 | 3 | 1 | 16 |
| 26 | 4 | 2 | 2 | 4 | 4 | 3 | 8 | 27 |
| 27 | 5 | 1 | 5 | 0 | 4 | 12 | 3 | 30 |
| 28 | 3 | 3 | 1 | 4 | 2 | 5 | 6 | 24 |
| 29 | 1 | 3 | 0 | 6 | 2 | 1 | 5 | 18 |
| 30 | 4 | 2 | 2 | 2 | 0 | 2 | 1 | 13 |
| 1 July | 0 | 2 | 1 | 0 | 0 | 2 | 6 | 11 |
| 2 | 0 | 0 | 0 | 9 | 1 | 2 | 4 | 16 |
| 3 | 0 | 1 | 0 | 0 | 0 | 5 | 4 | 10 |
| 4 | 0 | 1 | 2 | 0 | 0 | 7 | 0 | 10 |
| 5 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 5 |
| 6 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 4 |
| 7 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 8 |
| 8 | 0 | 0 | 1 | 0 | 1 | 2 | 0 | 4 |
| 9 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 |
| 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 4 |
| 12 | 0 | 0 | 0 | 0 | 0 | 7 | 2 | 9 |
| 13 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 |
| 14 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 15 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 4 |
| 16 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 |
| 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 18 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 |
| 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 22 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| 23 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| Totals | 33 | 32 | 23 | 42 | 26 | 79 | 53 | 288 |
| Median date of egg laying (June) | 27 | 28 | 27 | 29 | 26 | 28 | 28 | 28 |

**Appendix 11**
Dates of laying of first eggs known within 48 h at seven study plots in 1977

| Date of egg laying | Study plot | | | | | | | Totals |
|---|---|---|---|---|---|---|---|---|
| | G1 | G4 | N | Q1 | Q4 | S1 | U | |
| 21 June | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 |
| 22 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 |
| 23 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 |
| 24 | 3 | 1 | 0 | 2 | 1 | 1 | 0 | 8 |
| 25 | 3 | 1 | 1 | 0 | 0 | 2 | 2 | 9 |
| 26 | 1 | 4 | 0 | 1 | 1 | 4 | 2 | 13 |
| 27 | 2 | 0 | 0 | 1 | 0 | 3 | 1 | 7 |
| 28 | 3 | 1 | 0 | 2 | 3 | 8 | 4 | 21 |
| 29 | 3 | 8 | 0 | 0 | 0 | 7 | 4 | 22 |
| 30 | 0 | 2 | 5 | 0 | 0 | 4 | 7 | 18 |
| 1 July | 3 | 5 | 0 | 0 | 1 | 9 | 7 | 25 |
| 2 | 0 | 1 | 0 | 0 | 0 | 9 | 4 | 14 |
| 3 | 1 | 3 | 0 | 0 | 0 | 11 | 5 | 20 |
| 4 | 2 | 0 | 0 | 0 | 0 | 12 | 1 | 15 |
| 5 | 0 | 0 | 3 | 1 | 1 | 8 | 3 | 16 |
| 6 | 0 | 2 | 3 | 0 | 3 | 2 | 4 | 14 |
| 7 | 0 | 1 | 1 | 4 | 1 | 0 | 1 | 8 |
| 8 | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 6 |
| 9 | 3 | 2 | 0 | 3 | 0 | 1 | 1 | 10 |
| 10 | 0 | 0 | 0 | 1 | 0 | 6 | 2 | 9 |
| 11 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 |
| 12 | 2 | 1 | 0 | 1 | 1 | 3 | 1 | 9 |
| 13 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 4 |
| 14 | 2 | 1 | 0 | 1 | 2 | 2 | 0 | 8 |
| 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| 17 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 18 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 |
| 19 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 21 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 3 |
| 27 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 29 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| Totals | 33 | 39 | 14 | 17 | 14 | 106 | 52 | 275 |
| Median date of egg laying (July) | 1 | 1 | 5 | 7 | 5 | 3 | 1 | 2 |

## Appendix 12
Dates of hatching of first eggs at seven study plots in 1975

| Date of hatching | Study plot | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | G1 | G4 | N | Q1 | Q4 | S1 | U | Totals | Totals − Q4 |
| 24 July | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 25 | 1 | 4 | 1 | 3 | 2 | 5 | 8 | 24 | 22 |
| 26 | 4 | 8 | 8 | 4 | 7 | 5 | 1 | 37 | 30 |
| 27 | 6 | 1 | 6 | 4 | 8 | 7 | 9 | 41 | 33 |
| 28 | 6 | 6 | 6 | 2 | 4 | 17 | 6 | 47 | 43 |
| 29 | 4 | 3 | 7 | 3 | 4 | 17 | 2 | 40 | 36 |
| 30 | 3 | 2 | 6 | 4 | 4 | 17 | 10 | 46 | 42 |
| 31 | 2 | 4 | 6 | 30 | 14 | 23 | 7 | 86 | 72 |
| 1 August | 5 | 6 | 6 | 3 | 1 | 12 | 9 | 42 | 41 |
| 2 | 1 | 0 | 3 | 2 | 0 | 6 | 0 | 12 | 12 |
| 3 | 0 | 0 | 7 | 2 | 1 | 8 | 7 | 25 | 24 |
| 4 | 0 | 0 | 4 | 6 | 4 | 1 | 0 | 15 | 11 |
| 5 | 1 | 0 | 3 | 7 | 5 | 4 | 1 | 21 | 16 |
| 6 | 0 | 1 | 2 | 7 | 5 | 4 | 4 | 23 | 18 |
| 7 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| 8 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 4 | 4 |
| 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12 | 1 | 0 | 1 | 2 | 2 | 2 | 7 | 15 | 13 |
| 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 17 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| 18 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| Totals | 35 | 35 | 66 | 80 | 61 | 134 | 73 | 484 | 423 |
| Median date of hatching (J = July, A = August) | 29J | 28J | 30J | 31J | 31J | 30J | 30J | 31J | 31J |

**Appendix 13**
Dates of hatching of first eggs at 10 study plots in 1976

| Date of hatching | Study plot | | | | | | | | | | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | G1 | G4 | M | N | Q1 | Q4 | S1 | S2 | S3 | U | |
| 20 July | 1 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 6 |
| 21 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 5 |
| 22 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 5 |
| 23 | 3 | 5 | 2 | 3 | 3 | 0 | 5 | 1 | 0 | 1 | 23 |
| 24 | 1 | 4 | 2 | 1 | 0 | 5 | 2 | 2 | 1 | 0 | 18 |
| 25 | 3 | 4 | 1 | 3 | 1 | 1 | 4 | 7 | 6 | 3 | 33 |
| 26 | 2 | 0 | 1 | 10 | 6 | 17 | 11 | 7 | 4 | 2 | 60 |
| 27 | 9 | 7 | 7 | 4 | 5 | 13 | 7 | 5 | 4 | 1 | 62 |
| 28 | 10 | 4 | 4 | 14 | 1 | 0 | 12 | 2 | 2 | 1 | 50 |
| 29 | 0 | 0 | 0 | 1 | 1 | 0 | 9 | 1 | 0 | 0 | 12 |
| 30 | 1 | 0 | 0 | 0 | 0 | 0 | 6 | 7 | 0 | 12 | 26 |
| 31 | 0 | 1 | 13 | 25 | 0 | 0 | 19 | 6 | 7 | 6 | 77 |
| 1 August | 10 | 2 | 1 | 0 | 2 | 0 | 8 | 8 | 0 | 3 | 34 |
| 2 | 3 | 2 | 1 | 0 | 7 | 5 | 6 | 3 | 0 | 3 | 30 |
| 3 | 0 | 3 | 0 | 0 | 0 | 0 | 7 | 1 | 0 | 4 | 15 |
| 4 | 0 | 1 | 2 | 0 | 3 | 2 | 5 | 0 | 0 | 2 | 15 |
| 5 | 0 | 1 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 1 | 9 |
| 6 | 0 | 3 | 1 | 0 | 3 | 8 | 1 | 2 | 0 | 2 | 20 |
| 7 | 0 | 0 | 0 | 6 | 0 | 0 | 1 | 0 | 2 | 1 | 10 |
| 8 | 0 | 2 | 1 | 0 | 6 | 4 | 1 | 1 | 0 | 1 | 16 |
| 9 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 3 |
| 10 | 0 | 0 | 2 | 0 | 0 | 0 | 4 | 2 | 0 | 0 | 8 |
| 11 | 0 | 0 | 0 | 4 | 0 | 4 | 3 | 0 | 2 | 0 | 13 |
| 12 | 0 | 1 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 7 |
| 13 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 5 |
| 14 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 |
| 15 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 |
| 16 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 3 |
| 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 18 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 3 |
| 19 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 4 |
| 20 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 3 |
| 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 22 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| —* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 27 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| Totals | 46 | 44 | 40 | 76 | 47 | 62 | 137 | 58 | 30 | 45 | 585 |
| Median date of hatching (J = July, A = August) | 28J | 27J | † | 28J | 2A | 27J | 31J | † | † | 31J | 30J |

* No first eggs hatched between 22 and 27 August.
† Data incomplete due to fog and median therefore not calculated.

## Appendix 14
Dates of hatching of first eggs at seven study plots in 1977

| Date of hatching | Study plot | | | | | | | Totals |
|---|---|---|---|---|---|---|---|---|
| | G1 | G4 | N | Q1 | Q4 | S1 | U | |
| 23 July | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| 24 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 |
| 25 | 2 | 1 | 0 | 0 | 0 | 2 | 0 | 5 |
| 26 | 2 | 2 | 1 | 2 | 1 | 4 | 0 | 12 |
| 27 | 2 | 2 | 0 | 0 | 2 | 5 | 1 | 12 |
| 28 | 2 | 4 | 1 | 2 | 3 | 4 | 0 | 16 |
| 29 | 0 | 2 | 5 | 0 | 5 | 7 | 1 | 20 |
| 30 | 2 | 5 | 4 | 6 | 8 | 5 | 0 | 30 |
| 31 | 4 | 5 | 7 | 10 | 5 | 8 | 4 | 43 |
| 1 August | 4 | 1 | 6 | 3 | 6 | 14 | 5 | 39 |
| 2 | 3 | 1 | 0 | 3 | 8 | 9 | 4 | 28 |
| 3 | 2 | 1 | 0 | 3 | 7 | 12 | 1 | 26 |
| 4 | 4 | 2 | 6 | 10 | 5 | 16 | 4 | 47 |
| 5 | 3 | 3 | 9 | 3 | 7 | 7 | 3 | 35 |
| 6 | 2 | 1 | 7 | 5 | 2 | 8 | 3 | 28 |
| 7 | 3 | 3 | 8 | 12 | 2 | 5 | 3 | 36 |
| 8 | 0 | 2 | 4 | 6 | 1 | 8 | 2 | 23 |
| 9 | 2 | 1 | 1 | 3 | 0 | 2 | 1 | 10 |
| 10 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 6 |
| 11 | 0 | 0 | 0 | 5 | 0 | 6 | 2 | 13 |
| 12 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 5 |
| 13 | 2 | 0 | 3 | 1 | 1 | 1 | 1 | 9 |
| 14 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 3 |
| 15 | 1 | 0 | 3 | 1 | 1 | 4 | 0 | 10 |
| 16 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 3 |
| 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 18 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 3 |
| 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 20 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 22 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 |
| 23 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| Totals | 43 | 41 | 67 | 81 | 67 | 134 | 37 | 470 |
| Median date of hatching | 2A | 31J | 5A | 5A | 2A | 3A | 4A | 4A |

## Appendix 15
Dates of fledging of chicks at six study plots in 1975. The dates given are those of the day on which the chick was missing, fledging having presumably occurred during the previous night

| Date of fledging | Study plot | | | | | | Totals |
|---|---|---|---|---|---|---|---|
| | G1 | G4 | M | N | S1 | U | |
| 12 August | 0 | 3 | 1 | 0 | 3 | 3 | 10 |
| 13 | 0 | 4 | 1 | 1 | 0 | 1 | 7 |
| 14 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 15 | 0 | 0 | 5 | 0 | 3 | 5 | 13 |
| 16 | 9 | 12 | 3 | 10 | 10 | 15 | 59 |
| 17 | 3 | 2 | 5 | 3 | 11 | 3 | 27 |
| 18 | 4 | 6 | 4 | 6 | 22 | 5 | 47 |
| 19 | 2 | 2 | 2 | 1 | 1 | 2 | 10 |
| 20 | 0 | 0 | 3 | 4 | 0 | 0 | 7 |
| 21 | 12 | 4 | 5 | 8 | 17 | 13 | 59 |
| 22 | 0 | 0 | 0 | 8 | 9 | 7 | 24 |
| 23 | 3 | 3 | 2 | 6 | 16 | 1 | 31 |
| 24 | 4 | 1 | 3 | 1 | 9 | 0 | 18 |
| 25 | 1 | 1 | 0 | 2 | 0 | 0 | 4 |
| 26 | 2 | 1 | 3 | 12 | 14 | 4 | 36 |
| 27 | 0 | 1 | 0 | 0 | 4 | 2 | 7 |
| 28 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 29 | 0 | 0 | 0 | 0 | 3 | 0 | 3 |
| 30 | 0 | 0 | 1 | 2 | 4 | 2 | 9 |
| 31 | 3 | 0 | 0 | 0 | 2 | 1 | 6 |
| Totals | 43 | 40 | 38 | 64 | 130 | 64 | 379 |

**Appendix 16**
Dates of fledging of chicks at 10 study plots in 1976*

| Date of fledging | Study plot | | | | | | | | | | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | G1 | G4 | M | N | Q1 | Q4 | S1 | S2 | S3 | U | |
| 8 August | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 9 | 0 | 1 | — | 0 | — | — | 0 | 0 | 0 | 0 | 1 |
| 10 | 0 | 1 | 0 | 0 | — | — | 0 | 0 | — | 0 | 1 |
| 11 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | — | 0 | 3 |
| 12 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| 13 | 5 | 2 | 0 | 1 | 1 | 3 | 4 | 1 | 3 | 0 | 20 |
| 14 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 4 |
| 15 | 4 | 2 | 2 | 0 | — | — | 5 | 1 | — | 1 | 15 |
| 16 | 0 | 1 | 2 | 7 | 4 | 11 | 5 | 0 | 1 | 5 | 36 |
| 17 | 5 | 1 | 1 | 8 | 2 | 4 | 8 | 8 | 6 | 1 | 44 |
| 18 | 18 | 13 | 9 | 4 | 5 | 13 | 22 | 20 | 0 | 1 | 105 |
| 19 | 3 | 0 | 3 | 5 | 2 | 1 | 5 | 4 | 6 | 2 | 31 |
| 20 | 3 | 4 | 3 | 2 | 3 | 5 | 13 | 1 | 0 | 0 | 34 |
| 21 | 0 | 6 | 2 | 20 | 6 | 7 | 4 | 8 | 3 | 14 | 70 |
| 22 | 0 | 2 | 2 | 8 | 4 | 4 | 4 | 2 | — | 7 | 33 |
| 23 | 4 | 2 | 1 | 5 | 11 | 6 | 12 | 1 | 4 | 1 | 47 |
| 24 | 0 | 0 | 3 | 0 | 1 | 1 | 4 | 2 | 0 | 2 | 13 |
| 25 | 0 | 0 | — | — | — | — | 5 | 0 | — | 0 | 5 |
| 26 | 0 | 1 | 0 | 4 | 2 | 1 | 11 | 5 | 3 | 6 | 33 |
| 27 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 5 |
| 28 | 0 | 1 | 5 | 5 | 0 | 1 | 7 | 1 | 1 | 4 | 25 |
| 29 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 1 | 0 | 0 | 5 |
| 30 | 0 | 0 | 0 | 2 | 0 | 1 | 5 | 0 | 1 | 1 | 10 |
| 31 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1 September | 1 | 0 | 1 | 0 | 0 | 0 | 7 | 0 | — | 0 | 9 |
| 2 | 1 | 0 | 0 | 1 | 2 | 0 | 7 | 0 | 0 | 0 | 11 |
| 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| 4 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 |
| 5 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 |
| 6 | 1 | 0 | 0 | 0 | — | — | 0 | 0 | — | 0 | 1 |
| 7 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 4 |
| 8 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Totals | 45 | 40 | 37 | 78 | 44 | 60 | 138 | 57 | 29 | 46 | 574 |

* Dash indicates observations not possible due to fog.

## Appendix 17
Dates of fledging of chicks at seven study plots in 1977

| Date of fledging | Study plots | | | | | | | Totals |
|---|---|---|---|---|---|---|---|---|
| | G1 | G4 | N | Q1 | Q4 | S1 | U | |
| 13 August | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 14 | 4 | 1 | 1 | 1 | 0 | 5 | 0 | 12 |
| 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 |
| 17 | 4 | 6 | 0 | 3 | 4 | 3 | 0 | 20 |
| 18 | 2 | 4 | 0 | 1 | 1 | 9 | 1 | 18 |
| 19 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 20 | 2 | 0 | 0 | 3 | 3 | 0 | 0 | 8 |
| 21 | 1 | 6 | 14 | 10 | 15 | 13 | 3 | 62 |
| 22 | 2 | 1 | 1 | 3 | 0 | 9 | 3 | 19 |
| 23 | 11 | 5 | 29 | 18 | 22 | 35 | 8 | 128 |
| 24 | 3 | 2 | 3 | 9 | 4 | 13 | 4 | 38 |
| 25 | 0 | 1 | 0 | 0 | 1 | 3 | 0 | 5 |
| 26 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 5 |
| 27 | 5 | 4 | 11 | 7 | 6 | 6 | 6 | 45 |
| 28 | 0 | 1 | 8 | 8 | 3 | 8 | 2 | 30 |
| 29 | 0 | 0 | 2 | 3 | 1 | 0 | 0 | 6 |
| 30 | 0 | 1 | 0 | 1 | 1 | 3 | 0 | 6 |
| 31 | 0 | 1 | 0 | 1 | 0 | 2 | 3 | 7 |
| 1 September | 3 | 1 | 0 | 4 | 2 | 5 | 3 | 18 |
| 2 | 3 | 1 | 4 | 1 | 0 | 5 | 0 | 14 |
| 3 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 4 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 3 |
| 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6 | 2 | 0 | 3 | 0 | 0 | 1 | 0 | 6 |
| 7 | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 4 |
| 8 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Totals | 44 | 36 | 77 | 74 | 63 | 133 | 34 | 461 |

**Appendix 18**
Duration of chick rearing in relation to date of hatching at study plots G1, G4, S1, and U in 1975

| Date of hatching | Duration of chick-rearing period, days | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 |
| 24 July | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 25 | 0 | 0 | 0 | 7 | 3 | 0 | 4 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| 26 | 0 | 0 | 2 | 2 | 1 | 2 | 9 | 4 | 2 | 1 | 0 | 0 | 0 | 0 |
| 27 | 0 | 0 | 0 | 0 | 1 | 7 | 7 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| 28 | 0 | 1 | 0 | 0 | 22 | 5 | 7 | 0 | 0 | 12 | 2 | 1 | 1 | 0 |
| 29 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 2 | 3 | 0 | 0 | 0 | 0 |
| 30 | 0 | 0 | 4 | 5 | 15 | 1 | 0 | 13 | 2 | 10 | 0 | 0 | 4 | 0 |
| 31 | 0 | 0 | 3 | 5 | 2 | 0 | 6 | 4 | 9 | 4 | 0 | 1 | 0 | 1 |
| 1 August | 1 | 0 | 5 | 3 | 5 | 13 | 6 | 5 | 4 | 1 | 5 | 0 | 0 | 0 |
| 2 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 2 | 0 | 2 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0 | 1 | 3 | 4 | 2 | 1 | 2 | 5 | 1 | 0 | 1 | 0 | 0 |
| 4 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| 6 | 1 | 0 | 1 | 0 | 0 | 4 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| 7 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12 | 1 | 0 | 0 | 3 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 18 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Totals | 3 | 3 | 17 | 31 | 57 | 38 | 50 | 41 | 24 | 36 | 8 | 4 | 5 | 1 |

**Appendix 19**
Duration of chick rearing in relation to the date of hatching at all study plots in 1976

| Date of hatching | Duration of chick-rearing period, days | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30+ |
| 20 July | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| 22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| 23 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 3 | 2 | 0 | 5 | 1 | 1 | 1 | 1 |
| 24 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 4 | 4 | 1 | 0 | 0 | 1 | 0 |
| 25 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 5 | 3 | 4 | 0 | 1 | 0 | 0 | 0 | 0 |
| 26 | 0 | 0 | 2 | 2 | 1 | 3 | 12 | 5 | 9 | 1 | 6 | 1 | 2 | 0 | 0 | 1 |
| 27 | 0 | 0 | 0 | 0 | 2 | 4 | 6 | 15 | 3 | 4 | 6 | 1 | 1 | 0 | 0 | 1 |
| 28 | 0 | 1 | 1 | 1 | 3 | 5 | 11 | 5 | 3 | 8 | 1 | 2 | 0 | 0 | 1 | 0 |
| 29 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 3 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 30 | 0 | 0 | 0 | 1 | 2 | 1 | 2 | 9 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 31 | 0 | 2 | 1 | 8 | 3 | 4 | 10 | 7 | 5 | 3 | 2 | 0 | 0 | 3 | 0 | 2 |
| 1 August | 0 | 0 | 6 | 1 | 4 | 1 | 1 | 5 | 1 | 1 | 4 | 0 | 0 | 0 | 0 | 0 |
| 2 | 1 | 4 | 0 | 2 | 5 | 5 | 4 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0 | 1 | 2 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4 | 0 | 1 | 1 | 2 | 2 | 1 | 0 | 1 | 3 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| 5 | 0 | 0 | 1 | 1 | 0 | 1 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6 | 2 | 0 | 7 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 7 | 0 | 2 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11 | 0 | 0 | 2 | 2 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 14 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 15 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 18 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 19 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 20 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Totals | 3 | 13 | 26 | 32 | 38 | 35 | 61 | 64 | 39 | 32 | 24 | 13 | 6 | 5 | 3 | 6 |

## Appendix 20

Duration of chick rearing in relation to date of hatching at all study plots in 1977

| Date of hatching | Duration of chick-rearing period, days | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 |
| 23 July | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 24 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 25 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| 26 | 0 | 0 | 0 | 1 | 4 | 0 | 2 | 4 | 1 | 0 | 0 | 0 | 0 | 0 |
| 27 | 0 | 0 | 0 | 1 | 0 | 1 | 3 | 2 | 1 | 1 | 2 | 0 | 0 | 0 |
| 28 | 0 | 0 | 0 | 0 | 0 | 7 | 4 | 0 | 1 | 2 | 0 | 0 | 0 | 0 |
| 29 | 0 | 1 | 0 | 0 | 2 | 3 | 0 | 0 | 10 | 2 | 2 | 0 | 0 | 0 |
| 30 | 0 | 0 | 0 | 2 | 4 | 0 | 2 | 11 | 1 | 6 | 1 | 0 | 0 | 1 |
| 31 | 0 | 0 | 1 | 2 | 1 | 3 | 14 | 4 | 12 | 2 | 0 | 0 | 0 | 0 |
| 1 August | 0 | 0 | 1 | 0 | 0 | 16 | 4 | 16 | 1 | 0 | 0 | 0 | 0 | 0 |
| 2 | 0 | 0 | 0 | 0 | 1 | 2 | 8 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 3 | 0 | 0 | 1 | 0 | 3 | 26 | 5 | 0 | 0 | 3 | 1 | 0 | 0 | 0 |
| 4 | 0 | 0 | 3 | 1 | 25 | 5 | 2 | 1 | 6 | 1 | 0 | 0 | 0 | 0 |
| 5 | 0 | 1 | 1 | 9 | 9 | 2 | 1 | 9 | 0 | 3 | 1 | 0 | 0 | 0 |
| 6 | 2 | 0 | 4 | 9 | 0 | 1 | 7 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| 7 | 1 | 4 | 6 | 0 | 0 | 12 | 10 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 8 | 3 | 1 | 0 | 1 | 5 | 7 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 0 |
| 9 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 |
| 10 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11 | 0 | 1 | 3 | 1 | 3 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12 | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13 | 0 | 0 | 0 | 0 | 5 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 14 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 15 | 0 | 0 | 1 | 4 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 18 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 19 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 20 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 21 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Totals | 9 | 11 | 28 | 35 | 69 | 97 | 69 | 59 | 38 | 22 | 7 | 2 | 0 | 1 |

**Appendix 21**
Distribution of sites according to neighbour, wall, and slope characters at seven study plots for 1977 only*

| Study plot | No. of neighbours | | | | | No. of walls | | | | | Slope of ledge | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | None | One | Two | Three | Two & three | None | One | Two | Three | Two & three | Towards the sea | Level |
| G1 | 13(24.5) | 20(37.7) | 18(34.0) | 2(3.8) | 20(37.8) | 0 | 31(58.5) | 22(41.5) | | | 23(43.4) | 30(56.6) |
| G4 | 24(36.4) | 31(47.0) | 11(16.7) | | | 9(13.6) | 40(60.6) | 14(21.2) | 3(4.5) | 17(25.7) | 47(71.2) | 19(28.8) |
| N | 29(30.2) | 45(46.9) | 21(21.9) | 1(1.0) | 22(22.9) | 3(3.1) | 67(69.8) | 24(25.0) | 2(2.1) | 26(27.1) | 33(34.4) | 63(65.6) |
| Q1 | 35(35.4) | 43(43.4) | 21(21.2) | | | 6(6.0) | 58(58.6) | 35(35.4) | | | 34(34.3) | 65(65.7) |
| Q4 | 15(17.4) | 38(44.2) | 31(36.0) | 2(2.4) | 33(38.4) | 2(2.3) | 61(70.9) | 21(24.4) | 2(2.4) | 23(26.8) | 58(67.4) | 28(32.6) |
| S1 | 34(19.3) | 84(47.7) | 50(28.4) | 8(4.6) | 58(33.0) | 10(5.7) | 109(61.9) | 52(29.5) | 5(2.9) | 57(32.4) | 72(44.7) | 89(55.3) |
| U | 15(29.4) | 23(45.1) | 9(17.6) | 4(7.9) | 13(25.5) | 8(15.7) | 32(62.7) | 11(21.6) | | | 17(33.3) | 34(66.7) |

* Percentages are given in parentheses.

**Appendix 22**
Body weight (g) of individual chicks on growth plots in relation to age, 1975–77

| Study plot | Chick no. | Date of hatching | Plumage | Age, days* | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
| 1975: | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| SA | 01† | 26 July | — | — | 65 | — | 89 | — | — | 125 | — | — | 165 | — | — | 191 | (189) | — | 187 | — | — | 185 | — | 191 | — | — | — | — |
| | 02 | 25 | — | — | — | 102 | — | 128 | — | — | 161 | — | — | 173 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 03† | 26 | — | — | 77 | — | 97 | — | — | 148 | — | — | 173 | — | — | 211 | (209) | — | 204 | — | — | 205 | — | 209 | — | — | — | — |
| | 04 | 25 | — | — | — | (120) | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 05 | 26 | — | — | 71 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 06 | 27 | — | — | — | (113) | — | — | 127 | — | — | 161 | — | — | 185 | — | — | 178 | — | — | — | — | — | — | — | — | — | — |
| | 07† | 29 | — | 70 | (80) | — | 101 | — | — | 123 | — | — | — | — | — | 175 | (182) | — | 196 | — | 196 | — | 202 | — | — | 207 | — | — |
| | 08† | 28 | — | — | 67 | — | — | 97 | — | — | 125 | — | — | 153 | — | — | 187 | — | — | 188 | — | 208 | — | 187 | — | — | 218 | — |
| | 09 | 29 | — | 63 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 10† | 28 | — | — | 76 | — | — | 117 | — | — | 148 | — | — | 167 | — | — | 182 | — | — | 199 | — | 209 | — | 202 | — | — | — | — |
| | 11 | 30 | — | — | — | 90 | — | — | 131 | — | — | 160 | — | — | 154 | — | — | 186 | — | 200 | — | — | — | — | — | — | — | — |
| | 12 | 30 | — | — | — | 86 | — | — | 99 | — | — | 116 | — | — | 128 | — | — | 152 | — | — | — | — | — | — | — | — | — | — |
| | 13 | 30 | — | — | — | 82 | — | — | 125 | — | — | 177 | — | — | 229 | — | — | 207 | — | 222 | — | 223 | — | — | 222 | — | — | — |
| | 14 | 30 | — | — | — | 89 | — | — | — | — | — | 166 | — | — | 160 | — | — | 180 | — | 180 | — | 184 | — | — | 181 | — | — | — |
| | 15 | 30 | — | — | — | 88 | — | — | 113 | — | — | 182 | — | — | 164 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 16† | 31 | — | — | 66 | — | — | 115 | — | — | 137 | — | — | 140 | — | — | 147 | — | 162 | — | 154 | — | — | 184 | — | — | — | — |
| | 17 | 30 | — | — | — | 89 | — | — | 129 | — | — | 153 | — | — | 178 | — | — | 199 | — | 201 | — | 201 | — | — | — | — | — | — |
| SB | 01 | 26 | — | 67 | — | — | 113 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 02 | 25 | — | — | (95) | — | — | 124 | — | — | 177 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 03† | 28 | — | — | 68 | — | — | 118 | — | — | 159 | — | — | 183 | — | — | 170 | — | — | 189 | — | — | — | — | — | — | — | — |
| | 04† | 28 | — | — | 70 | — | — | 98 | — | — | 124 | — | — | 139 | — | — | 147 | — | — | 176 | — | 172 | — | 179 | — | — | — | — |
| | 05† | 28 | — | — | 66 | — | — | 89 | — | — | 129 | — | — | 138 | — | — | 159 | — | — | 174 | — | 154 | — | 174 | — | — | 179 | — |
| | 06† | 28 | — | — | 71 | — | — | 97 | — | — | 153 | — | — | 176 | — | — | 198 | — | — | 220 | — | 206 | — | 205 | — | — | — | — |
| | 07 | 29 | — | 64 | — | — | — | — | — | — | — | — | — | — | — | 177 | — | — | 162 | — | 187 | — | 191 | — | — | — | — | — |
| | 08† | 31 | — | — | 79 | — | — | 120 | — | — | 146 | — | — | 177 | — | — | 187 | — | — | — | — | — | — | — | — | — | — | — |
| | 09† | 31 | — | — | 76 | — | — | 115 | — | — | 147 | — | — | 154 | — | — | 166 | — | 175 | — | 186 | — | — | 195 | — | — | — | — |
| | 10† | 12 August | — | — | 68 | — | 75 | — | — | 103 | — | 120 | — | — | 174 | — | (182) | 186 | — | — | — | — | — | — | — | — | — | — |
| | 11 | 20 | — | 61 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| SC | 01 | 26 July | — | — | 63 | — | 75 | — | — | — | — | — | 136 | — | — | 202 | — | — | — | — | — | — | — | — | — | — | — | — |
| | 02 | 26 | — | 68 | 80 | — | 98 | — | — | 150 | — | — | 175 | — | — | 198 | — | — | — | — | — | — | — | — | — | — | — | — |
| | 03† | 26 | — | 56 | 75 | — | 91 | — | — | 139 | — | — | 169 | — | — | 203 | (210) | — | 223 | — | — | 226 | — | — | — | — | — | — |
| | 04† | 26 | — | 59 | 68 | — | — | — | — | — | — | — | 169 | — | — | 189 | (186) | — | 181 | — | — | — | — | — | — | — | — | — |
| | 05† | 27 | — | 68 | (76) | 84 | — | — | 126 | — | — | — | — | — | 202 | — | (208) | — | — | — | 202 | — | 237 | — | — | — | — | — |
| | 06† | 25 | — | — | 84 | 101 | — | 141 | — | — | 215 | — | — | 247 | — | — | 258 | — | — | 227 | — | — | — | — | — | — | — | — |
| | 07† | 26 | — | — | 70 | — | 77 | — | — | 121 | — | — | 160 | — | — | 178 | (191) | — | 215 | — | — | 203 | — | — | — | — | — | — |
| | 08 | 29 | — | 63 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 09 | 29 | — | 55 | (68) | — | — | — | — | 131 | — | — | 125 | — | — | 152 | — | — | 178 | — | 169 | — | 169 | — | — | 187 | — | — |
| | 10 | 28 | — | — | 68 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 11 | 31 | — | — | 71 | — | — | 103 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 12 | 30 | — | — | — | 90 | — | — | 123 | — | — | — | — | — | 176 | — | — | 170 | — | — | — | 186 | — | — | 206 | — | — | — |

Appendix 22 (cont'd)

| Study plot | Chick no. | Date of hatching | Plumage | Age, days* | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
| | 13 | 30 | — | — | — | 92 | — | — | 139 | — | — | 173 | — | — | 191 | — | — | 192 | — | 198 | — | — | — | — | — | — | — | — |
| | 14 | 30 | — | — | — | 107 | — | — | 140 | — | — | 163 | — | — | 178 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 15 | 26 | — | 70 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 1976: | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| SA | 01† | 23 July | — | 70 | (76) | — | — | — | — | — | — | — | 165 | — | — | 174 | (179) | — | 189 | — | — | 200 | — | — | 188 | — | — | 210 |
| | 02† | 24 | — | 67 | (73) | 86 | 111 | — | — | 146 | — | 159 | — | — | 173 | — | (178) | 180 | — | — | 199 | — | — | 193 | — | — | — | — |
| | 03† | 24 | — | 66 | (72) | 81 | 90 | — | — | 115 | — | 150 | — | — | 168 | — | (179) | 184 | — | — | 220 | — | — | 212 | — | — | 220 | — |
| | 04† | 25 | — | — | 74 | 82 | — | — | 103 | — | 119 | — | — | 139 | — | — | 150 | — | — | 172 | — | — | 194 | — | — | 211 | — | — |
| | 05† | 26 | — | 60 | 80 | — | — | 124 | — | 125 | — | — | 175 | — | — | 198 | (200) | — | 205 | — | — | 203 | — | — | 209 | — | — | — |
| | 06† | 26 | — | 62 | 71 | — | — | 107 | — | 159 | — | — | 170 | — | — | 189 | (194) | — | 203 | — | — | 212 | — | — | 225 | — | — | — |
| | 07† | 26 | — | 68 | 62 | — | — | 104 | — | 131 | — | — | 148 | — | — | 172 | (171) | — | 168 | — | — | 197 | — | — | 211 | — | — | — |
| | 08† | 27 | — | 69 | (84) | — | 114 | — | 113 | — | — | 156 | — | — | 155 | — | (172) | 180 | — | — | 175 | — | — | 218 | — | — | — | — |
| | 09† | 27 | — | 68 | (77) | — | 97 | — | — | — | — | 146 | — | — | 176 | — | (199) | 211 | — | — | 200 | — | — | 251 | — | — | — | — |
| | 10† | 28 | — | 74 | (82) | 90 | — | 111 | — | — | 129 | — | — | 126 | — | — | 139 | — | — | 161 | — | — | 184 | — | — | 186 | — | — |
| | 11 | 31 | — | — | 69 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 208 | — | — | — | — | — |
| | 12 | 28 | — | 68 | — | 94 | — | 100 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 13 | 29 | — | — | 75 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 14 | 4 August | — | 68 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| SB | 01† | 25 July | — | — | 83 | 97 | 102 | — | 113 | — | 136 | — | — | 158 | — | — | 165 | — | — | 175 | — | — | 188 | — | — | 190 | — | — |
| | 02† | 27 | — | 70 | 70 | — | 95 | — | 105 | — | — | 136 | — | — | — | — | (154) | 160 | — | — | 178 | — | — | 197 | — | — | — | — |
| | 03† | 28 | — | 70 | (81) | 93 | — | 111 | — | — | 161 | — | — | 152 | — | — | 153 | — | — | 171 | — | — | 218 | — | — | 213 | — | — |
| | 04† | 29 | — | — | 83 | — | 125 | — | — | 158 | — | — | 184 | — | — | 203 | (216) | — | 241 | — | — | — | — | — | — | — | — | — |
| | 05 | 30 | — | 72 | — | 63 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 06 | 30 | — | 64 | — | 74 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 07 | 15 August | — | — | 60 | — | — | 90 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| SC | 01† | 22 July | — | 77 | 78 | — | — | 100 | 93 | — | — | 119 | — | 138 | — | — | 145 | — | — | 187 | — | — | 197 | — | — | — | — | — |
| | 02† | 23 | — | 75 | (83) | — | 99 | 104 | — | — | 143 | — | 175 | — | — | 187 | (195) | — | 210 | — | — | 200 | — | — | 236 | — | — | — |
| | 03† | 23 | — | 71 | (86) | — | 117 | 102 | — | — | 177 | — | 149 | — | — | 171 | (171) | — | 170 | — | — | 216 | — | — | 186 | — | — | 153 |
| | 04† | 23 | — | 68 | (78) | — | 98 | 129 | — | — | 168 | — | 220 | — | — | 209 | (214) | — | 224 | — | — | — | — | — | — | — | — | — |
| | 05† | 24 | — | 64 | (62) | 60 | 64 | — | — | 90 | — | 139 | — | — | 157 | — | (169) | 175 | — | — | 191 | — | — | 209 | — | — | 216 | — |
| | 06† | 24 | — | 71 | (79) | 88 | 92 | — | — | 141 | — | 168 | — | — | 173 | — | (184) | 193 | — | — | 209 | — | — | — | — | — | — | — |
| | 07† | 26 | — | 63 | 73 | — | — | 107 | — | 121 | — | — | 185 | — | — | 204 | (203) | — | 200 | — | — | 191 | — | — | 228 | — | — | — |
| | 08† | 26 | — | 62 | 67 | — | — | 103 | — | 145 | — | — | 156 | — | — | 162 | (164) | — | 167 | — | — | 179 | — | — | 189 | — | — | — |
| | 09† | 26 | — | 52 | 54 | — | — | 85 | — | 96 | — | — | 132 | — | — | 141 | (149) | — | 164 | — | — | 163 | — | — | 186 | — | — | — |
| | 10† | 26 | — | 67 | 69 | — | — | 99 | — | 118 | — | — | 126 | — | — | 149 | (157) | — | 172 | — | — | 202 | — | — | 225 | — | — | 240 |
| | 11† | 25 | — | — | 77 | 91 | — | — | 120 | — | 141 | — | — | 160 | — | — | 157 | — | — | 172 | — | — | 183 | — | — | — | — | — |
| | 12† | 28 | — | 70 | (78) | 87 | — | 100 | — | — | 117 | — | — | 125 | — | — | 168 | — | — | 163 | — | — | 184 | — | — | — | — | — |
| | 13† | 30 | — | 71 | — | — | — | — | 110 | — | — | 137 | — | — | 169 | — | (182) | 189 | — | — | 203 | — | — | 230 | — | — | — | — |
| | 14† | 30 | — | 62 | (80) | 99 | — | — | 130 | — | — | 166 | — | — | 172 | — | (178) | 180 | — | — | 197 | — | — | 202 | — | — | — | — |
| | 15 | 22 | — | 74 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 16 | 22 | — | 81 | 98 | — | — | 114 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |

**Appendix 22** (cont'd)

| Study plot | Chick no. | Date of hatching | Plumage | Age, days* | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
| | 17 | 26 | — | — | 69 | — | — | 91 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 18 | 24 | — | — | — | — | 115 | — | — | 138 | — | 126 | — | — | 133 | — | — | 152 | — | — | — | — | — | — | — | — | — | — |
| | 19 | 28 | — | 72 | — | — | — | 94 | — | — | 102 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 20 | 29 | — | — | 87 | — | 90 | — | — | 107 | — | — | 145 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 21 | 1 August | — | 62 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 22 | 1 | — | 72 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 1977: | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| SA | 01† | 26 July | S | — | 66 | — | 101 | — | 112 | — | 136 | — | 190 | — | 199 | — | 212 | — | — | — | — | — | — | — | — | — | — | — |
| | 02† | 28 | W | — | 60 | — | 74 | — | 103 | — | 116 | — | 140 | — | 154 | — | (180) | 194 | (196) | 197 | (205) | — | 220 | — | 215 | — | — | — |
| | 03† | 28 | S | — | 57 | — | 83 | — | 104 | — | 140 | — | 144 | — | 165 | — | (184) | 193 | (195) | 200 | (204) | — | 213 | — | — | — | — | — |
| | 04† | 1 August | S | — | 64 | — | 86 | — | 106 | — | 137 | — | (160) | 171 | (188) | 205 | (207) | — | 211 | — | 235 | — | 238 | — | 240 | — | — | — |
| | 05† | 1 | S | — | 73 | — | 88 | — | 122 | — | 142 | — | (155) | 162 | (169) | 175 | (179) | — | 186 | — | 178 | — | — | — | — | — | — | — |
| | 06† | 1 | S | — | 77 | — | 95 | — | 110 | — | 144 | — | (165) | 175 | (167) | 158 | (169) | — | 191 | — | 180 | — | 180 | — | 190 | — | — | — |
| | 07† | 1 | S | — | 63 | — | 90 | — | 104 | — | 148 | — | (157) | 162 | (176) | 189 | (197) | — | 214 | — | 215 | — | 209 | — | 230 | — | — | — |
| | 08† | 5 | W | — | 82 | — | 100 | — | (133) | 150 | (168) | 186 | (192) | — | 204 | — | 212 | — | — | — | — | — | — | — | — | — | — | — |
| | 09† | 7 | W | — | 67 | — | (81) | 88 | (97) | 106 | (109) | — | 115 | — | 125 | — | 128 | — | 151 | — | 170 | — | 171 | — | — | — | — | — |
| | 10† | 7 | W | — | 75 | — | (109) | 126 | — | — | — | — | 186 | — | 212 | — | 223 | — | 245 | — | 256 | — | 272 | — | — | — | — | — |
| | 11 | 10 | — | — | 56 | — | 70 | — | (105) | 123 | (127) | 130 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 12 | 14 | S | — | — | 75 | (79) | 82 | (94) | 106 | (24) | 141 | (150) | 167 | (184) | 200 | (209) | 218 | (211) | 203 | — | — | — | — | — | — | — | — |
| SB | 01† | 30 July | S | — | 69 | — | 79 | — | 117 | — | 143 | — | 161 | — | (196) | 214 | (221) | 228 | (226) | — | 221 | — | 202 | — | — | — | — | — |
| | 02 | 1 August | — | — | 71 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 03 | 1 | — | — | 68 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 04 | 3 | — | — | 79 | — | 100 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 05† | 5 | W | — | 78 | — | 100 | — | (135) | 153 | (168) | 182 | (196) | — | 225 | — | 242 | — | 239 | — | 255 | — | 226 | — | — | — | — | — |
| | 06† | 5 | S | — | 91 | — | 108 | — | (128) | 138 | (160) | 182 | (183) | — | 185 | — | 198 | — | 210 | — | 220 | — | — | — | — | — | — | — |
| | 07† | 5 | S | — | 79 | — | 119 | — | (136) | 144 | (163) | 186 | (195) | — | 213 | — | 219 | — | 212 | — | 231 | — | — | — | — | — | — | — |
| | 08 | 7 | — | — | 74 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 09 | 11 | — | 54 | (61) | 68 | (80) | — | 105 | — | 135 | — | 157 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 10 | 9 | W | — | — | 83 | (95) | 106 | (121) | — | 152 | — | 145 | — | 181 | — | 201 | — | 226 | — | 238 | — | — | — | — | — | — | — |
| | 11 | 19 | — | — | 56 | — | 70 | — | 84 | — | 122 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 12 | 19 | — | — | 64 | — | 80 | — | 111 | — | 146 | — | 150 | — | 168 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| SC | 01† | 24 July | S | — | 64 | — | 96 | — | 123 | — | 140 | — | 179 | — | 200 | — | 225 | — | 237 | — | (250) | 256 | (243) | 230 | — | — | — | — |
| | 02† | 28 | — | — | 54 | — | 75 | — | 91 | — | 126 | — | 112 | — | 140 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 03 | 28 | — | — | 68 | — | 87 | — | 102 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 04 | 28 | — | — | 63 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 05 | 28 | — | — | 65 | — | 92 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 06 | 30 | — | — | 65 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 07† | 31 | S | 51 | (81) | 110 | (138) | 166 | (178) | 189 | (196) | 203 | (209) | — | 222 | — | 218 | — | — | — | — | — | — | — | — | — | — | — |
| | 08† | 30 | S | — | 54 | — | 62 | — | 98 | — | 105 | — | 133 | — | (144) | 150 | (163) | 175 | (188) | — | 215 | — | 209 | — | 195 | — | — | — |
| | 09 | 30 | W | — | 75 | — | 107 | — | 124 | — | 146 | — | 152 | — | (163) | 169 | (172) | 175 | (177) | — | 181 | — | 187 | — | — | — | — | — |
| | 10† | 30 | S | — | 62 | — | 82 | — | 126 | — | 149 | — | 200 | — | (209) | 213 | (231) | 248 | (253) | — | 262 | — | — | — | — | — | — | — |

**Appendix 22** (cont'd)

| Study plot | Chick no. | Date of hatching | Plumage | Age, days* | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
| | 11† | 1 August | S | — | 78 | — | — | — | — | — | 105 | — | (135) | 145 | (148) | 150 | (152) | — | 157 | — | 174 | — | 187 | — | — | — | — | — |
| | 12† | 3 | S | — | 62 | — | 32 | — | 127 | — | (151) | 163 | (165) | 170 | (184) | — | 212 | — | 240 | — | 232 | — | 252 | — | — | — | — | — |
| | 13† | 3 | S | — | 74 | — | — | — | — | — | — | 180 | (188) | 205 | (221) | — | 253 | — | 268 | — | 264 | — | 252 | — | — | — | — | — |
| | 15 | 5 | — | — | 80 | — | 99 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 16† | 6 | S | 66 | (74) | 81 | (97) | — | 130 | — | 153 | — | (164) | 170 | (176) | 181 | (188) | 194 | (192) | 190 | — | — | — | — | — | — | — | — |
| | 17† | 11 | S | 61 | (66) | 70 | (80) | — | 99 | — | 149 | — | 133 | — | 178 | — | 202 | — | 212 | — | 210 | — | 214 | — | — | — | — | — |
| | 18† | 17 | S | — | 80 | — | 92 | — | 110 | — | 134 | — | 160 | — | 200 | — | 197 | — | — | — | — | — | — | — | — | — | — | — |
| | 32 | — | — | — | — | — | — | — | — | — | — | — | — | 157 | — | 187 | — | 200 | (191) | 182 | (204) | 225 | (222) | 219 | — | — | — | — |
| SD | 01 | 26 July | S | — | 78 | — | 97 | — | 125 | — | 152 | — | 169 | — | 199 | — | 210 | — | (216) | 219 | (234) | 248 | — | — | — | — | — | — |
| | 02 | 26 | S | — | 72 | — | 111 | — | 143 | — | 170 | — | 197 | — | 261 | — | 261 | — | (276) | 284 | (279) | 275 | (279) | 282 | — | — | — | — |
| | 03 | 28 | S | — | 64 | — | 73 | — | 103 | — | 140 | — | 166 | — | 175 | — | (210) | 228 | (232) | 235 | — | — | — | — | — | — | — | — |
| | 04 | 28 | S | — | 67 | — | 89 | — | 108 | — | 150 | — | 175 | — | 199 | — | (233) | 250 | (256) | 262 | (270) | — | 286 | — | 275 | — | — | — |
| | 05 | 28 | S | — | 65 | — | 89 | — | 116 | — | 154 | — | 177 | — | 191 | — | (216) | 229 | (232) | 235 | (246) | — | 267 | — | — | — | — | — |
| | 06 | 31 | — | 56 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 07 | 30 | S | — | 64 | — | 91 | — | 91 | — | 118 | — | 143 | [illegible] | (181) | 200 | (190) | 180 | (184) | — | 193 | — | — | — | — | — | — | — |
| | 08 | 30 | S | — | 58 | — | 86 | — | 95 | — | 139 | — | 134 | [illegible] | [illegible]63) | 177 | (171) | 165 | (182) | — | 217 | — | 180 | — | — | — | — | — |
| | 09 | 30 | S | — | 73 | — | 94 | — | 135 | — | 159 | — | 185 | — | [illegible]84) | 184 | (190) | 195 | (198) | — | 205 | — | — | — | — | — | — | — |
| | 10 | 30 | W | — | 63 | — | 88 | — | 123 | — | 151 | — | 166 | — | (186) | 196 | (200) | 203 | (211) | — | 228 | — | — | — | — | — | — | — |
| | 11 | 1 August | W | — | 78 | — | 105 | — | 119 | — | 150 | — | (160) | 165 | (178) | 190 | (201) | — | 224 | — | 240 | — | 220 | — | 239 | — | — | — |
| | 12 | 1 | S | — | 76 | — | 101 | — | 131 | — | 135 | — | (162) | 175 | (174) | 173 | (186) | — | 212 | — | 235 | — | 235 | — | 245 | — | — | — |
| | 13 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 14 | 3 | S | — | 68 | — | 94 | — | 105 | — | (132) | 146 | (148) | 150 | — | — | — | — | — | — | 173 | — | — | — | — | — | — | — |
| | 15 | 3 | W | — | 67 | — | 97 | — | — | — | — | 143 | (146) | 160 | (168) | — | 184 | — | 190 | — | 202 | — | 206 | — | — | — | — | — |
| | 16 | 4 | S | — | (79) | — | (103) | 121 | (139) | — | 175 | — | 190 | — | (211) | 221 | (221) | 220 | (235) | 250 | (254) | 258 | — | — | — | — | — | — |
| | 17 | 3 | W | — | 60 | — | 92 | — | 106 | — | (134) | 148 | (155) | 162 | (176) | — | 204 | — | 235 | — | 233 | — | 241 | — | — | — | — | — |
| | 18 | 5 | — | — | 89 | — | 111 | — | (147) | 165 | (165) | 165 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 19 | 7 | S | — | 61 | — | (76) | 84 | (95) | 105 | (116) | — | 139 | — | 165 | — | 200 | — | 211 | — | 195 | — | 199 | — | — | — | — | — |
| | 20 | 7 | — | — | 55 | — | (56) | 56 | (50) | 45 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 21 | 15 | — | — | 73 | — | 78 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 33 | 17 | — | — | 65 | — | 87 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| GA | 01 | 26 July | S | — | 67 | — | 90 | — | 109 | — | 125 | — | 156 | — | 190 | — | 193 | — | (220) | 233 | — | — | — | — | — | — | — | — |
| | 02 | 28 | — | — | 93 | — | 111 | — | 137 | — | 159 | — | 179 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 03 | 28 | S | — | 65 | — | 91 | — | 103 | — | 133 | — | 155 | — | 181 | — | (198) | 207 | (215) | — | 231 | — | 225 | — | — | — | — | — |
| | 04 | 31 | S | 63 | (67) | 71 | (90) | 108 | (124) | 140 | (145) | 149 | (158) | — | 175 | — | (195) | 205 | — | 216 | (214) | — | — | 211 | — | — | — | — |
| | 05 | 1 August | S | — | 64 | — | 105 | — | 131 | — | 155 | — | (169) | 176 | (181) | — | 190 | — | 191 | — | (199) | — | 208 | — | 224 | — | — | — |
| | 06 | 3 | S | — | 63 | — | 76 | — | 122 | — | (116) | 118 | (119) | — | 200 | — | 197 | — | (209) | — | 221 | — | 257 | — | 265 | — | — | — |
| | 07 | 30 July | S | — | 63 | — | 80 | — | 116 | — | 126 | — | 133 | — | (140) | 143 | (152) | — | 170 | — | 202 | — | (199) | — | 196 | — | — | — |
| | 08 | 3 August | S | — | 80 | — | 127 | — | 139 | — | (150) | 155 | (172) | — | 205 | — | 180 | — | (202) | — | 223 | — | 234 | — | — | — | — | — |
| | 09 | 4 | S | 88 | (90) | 91 | 96 | 100 | (110) | — | 130 | — | (150) | 160 | (168) | 177 | (188) | — | (210) | 222 | — | — | — | — | — | — | — | — |
| | 10 | 5 | — | — | 55 | — | 100 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 11 | 9 | S | — | — | 93 | (104) | — | 125 | — | 150 | — | (170) | — | 191 | — | 207 | — | 214 | — | 213 | — | — | — | — | — | — | — |

**Appendix 22** (cont'd)

| Study plot | Chick no. | Date of hatching | Plumage | Age, days* | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
| | 12 | 2 | S | 68 | (78) | 88 | (103) | 118 | (126) | 133 | (134) | — | 134 | — | (155) | 165 | (181) | 196 | (200) | — | (211) | 213 | — | — | — | — | — | — |
| | 13 | 11 | — | 52 | (63) | — | 85 | — | 126 | — | — | — | — | — | 163 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| GB | 02 | 27 July | S | 63 | (72) | 81 | (94) | 107 | (119) | 130 | (145) | 160 | (168) | 177 | (178) | 182 | (184) | — | 187 | — | (207) | 216 | (208) | 201 | — | — | — | — |
| | 03 | 26 | — | — | 71 | — | 92 | — | 129 | — | 136 | — | 150 | — | 162 | — | 170 | — | (172) | 173 | (181) | — | 197 | — | — | — | — | — |
| | 04 | 28 | S | — | 70 | — | 99 | — | 115 | — | 146 | — | 169 | — | 168 | — | (183) | 190 | (195) | — | 205 | — | 208 | — | — | — | — | — |
| | 05 | 28 | S | — | 75 | — | 100 | — | 116 | — | 134 | — | 154 | — | 178 | — | (179) | 180 | (188) | — | 203 | — | 196 | — | — | — | — | — |
| | 06 | 28 | — | — | 78 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 07 | 28 | S | — | 67 | — | 79 | — | 110 | — | 130 | — | 150 | — | 146 | — | (159) | 166 | (172) | — | 183 | — | 181 | — | — | — | — | — |
| | 08 | 28 | S | — | 72 | — | 95 | — | 123 | — | 143 | — | 179 | — | 192 | — | (203) | 208 | (213) | — | 224 | — | 200 | — | — | — | — | — |
| | 09 | 30 | S | — | 81 | — | 109 | — | 149 | — | 166 | — | 180 | — | (203) | 215 | (229) | — | 258 | — | 222 | — | — | — | — | — | — | — |
| | 10 | 31 | S | 65 | (73) | 81 | (85) | 88 | (99) | 109 | (124) | 139 | (144) | — | 155 | — | — | — | — | 170 | (170) | — | (169) | 169 | — | — | — | — |
| | 11 | 31 | S | 62 | (65) | 68 | (75) | 81 | (97) | 112 | (121) | 129 | (128) | — | 126 | — | (143) | 152 | (159) | 166 | — | — | — | — | — | — | — | — |
| | 12 | 30 | — | — | 74 | — | 93 | — | 121 | — | 147 | — | 145 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 13 | 30 | S | — | 64 | — | 86 | — | 124 | — | 125 | — | 137 | — | (152) | 160 | (173) | — | 200 | — | 196 | — | — | — | — | — | — | — |
| | 14 | 30 | W | — | 77 | — | 99 | — | 108 | — | 168 | — | 167 | — | (167) | 167 | (185) | — | 222 | — | 208 | — | — | — | 270 | — | — | — |
| | 15 | 30 | S | — | 72 | — | 91 | — | 121 | — | 133 | — | 160 | — | (176) | 184 | (198) | — | 225 | — | 233 | — | — | — | — | — | — | — |
| | 16 | 2 August | S | 69 | (79) | 88 | (103) | 117 | (129) | 140 | (144) | — | 151 | — | (184) | 200 | (194) | 187 | (186) | — | — | 185 | — | — | — | — | — | — |
| | 17 | 3 | S | — | 62 | — | 95 | — | 108 | — | (115) | 118 | (128) | — | 148 | — | 166 | — | (169) | — | 172 | — | — | — | — | — | — | — |
| | 18 | 3 | S | — | 68 | — | 86 | — | 110 | — | (121) | 126 | (135) | — | 152 | — | 156 | — | (166) | — | 176 | — | 183 | — | — | — | — | — |
| | 19 | 3 | S | — | 64 | — | 86 | — | — | — | — | 140 | (152) | — | 175 | — | 170 | — | (182) | — | 193 | — | 209 | — | — | — | — | — |
| | 20 | 4 | S | 62 | (70) | 77 | (94) | 111 | (107) | — | 98 | — | (138) | 158 | (165) | 171 | (173) | — | (178) | 180 | (182) | 184 | — | — | — | — | — | — |
| | 21 | 3 | S | — | 58 | — | (85) | — | 112 | — | (127) | 135 | (149) | — | 177 | — | 171 | — | (179) | — | 188 | — | 210 | — | — | — | — | — |
| | 22 | 3 | — | — | 78 | — | 103 | — | 100 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 23 | 6 | S | 58 | (67) | 76 | (86) | — | 107 | — | (156) | 180 | — | — | — | — | — | 220 | (229) | 238 | (234) | 230 | (231) | 232 | — | — | — | — |
| | 24 | 5 | S | — | 82 | — | 98 | — | (123) | 135 | (153) | — | 190 | — | 190 | — | (201) | — | 212 | — | 223 | — | — | — | — | — | — | — |
| | 25 | 6 | S | 64 | — | — | — | — | 103 | — | (134) | 150 | (156) | 163 | (170) | — | (185) | 192 | (199) | 205 | (209) | 212 | (212) | 212 | — | — | — | — |
| | 26 | 5 | S | — | 60 | — | 72 | — | (103) | 119 | (135) | — | 166 | — | — | — | — | — | 180 | — | — | — | — | — | — | — | — | — |
| | 27 | 6 | S | 62 | (64) | 65 | (78) | — | 105 | — | (130) | 143 | (155) | 166 | (167) | — | (169) | 170 | (178) | 185 | (197) | 208 | (210) | 211 | — | — | — | — |
| | 28 | 5 | S | — | 60 | — | 80 | — | (105) | 117 | (128) | — | 151 | — | 165 | — | (167) | — | 168 | — | 196 | — | — | — | — | — | — | — |
| | 29 | 7 | S | — | 81 | — | (104) | 116 | (125) | — | 142 | — | 160 | — | (154) | — | 149 | — | 183 | — | 188 | — | 198 | — | — | — | — | — |
| | 32 | 12 | — | — | — | 90 | (87) | 84 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| GC | 01 | 2 | — | 52 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 02 | 2 | — | 61 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 03 | 5 | S | — | 67 | — | 93 | — | (123) | 138 | (140) | — | 143 | — | 157 | — | (167) | — | 178 | — | 185 | — | — | — | — | — | — | — |
| | 04 | 6 | S | 64 | (71) | 77 | (90) | — | 117 | — | (140) | 151 | (166) | 197 | (194) | — | (186) | 183 | (190) | 196 | — | — | — | — | — | — | — | — |
| | 05 | 7 | S | — | 66 | — | (85) | 95 | (106) | — | 128 | — | — | — | — | — | 164 | — | 200 | — | 216 | — | 222 | — | — | — | — | — |
| | 06 | 13 | W | — | 83 | — | 110 | — | — | — | 143 | — | 157 | — | 187 | — | 198 | — | 218 | — | 226 | — | — | — | — | — | — | — |
| | 07 | 13 | S | — | 75 | — | 89 | — | — | — | 110 | — | 126 | — | 161 | — | 188 | — | 202 | — | 195 | — | — | — | — | — | — | — |
| | 08 | 21 | — | — | 69 | — | 128 | — | 138 | — | 170 | — | 201 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | 15 | 15 | S | — | 59 | — | (81) | — | 103 | — | 123 | — | 156 | — | 194 | — | 221 | — | 247 | — | — | — | — | — | — | — | — | — |

* Figures in parentheses are interpolated.

† Chick data used in preparation of Table 56.

**Appendix 23**
Mean number of meals per 4-h period to chicks on study plot S1 in 1977 in relation to age and date of hatching. Diagonal lines connect rates observed on the same date

| Date of hatching | Chick age, days* | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1–3 | 4–6 | 7–9 | 10–12 | 13–15 | 16–18 | 19–21 |
| 26–28 July | 0.89(9)* | 0.89(9) | 0.78(9) | 0.89(9) | 0.78(9) | 0.56(9) | 0.71(7) |
| 29–31 | 1.00(15) | 0.80(15) | 1.00(15) | 0.69(16) | 0.67(15) | 0.71(14) | 0.64(11) |
| 1–3 August | 1.00(29) | 0.63(30) | 0.69(29) | 0.76(29) | 0.72(29) | 0.82(28) | 0.58(24) |
| 4–6 | 0.91(23) | 0.42(24) | 0.96(23) | 0.87(24) | 0.58(24) | 0.82(22) | 0.56(9) |
| 7–9 | 0.54(13) | 0.93(14) | 0.62(13) | 0.85(13) | 0.71(14) | 1.00(8) | 0.67(6) |
| 10–12 | 1.18(6) | 1.12(8) | 0.87(8) | 0.25(8) | 0.56(9) | 0.62(8) | 0.33(6) |
| 13–15 | 0.71(7) | 0.57(7) | 0.71(7) | 0.67(6) | 0.86(7) | 0.71(7) | |
| 16–18 | 0(3) | 0(3) | 1.33(3) | 1.00(3) | 1.00(3) | | |
| 19–21 | 1.00(6) | 0.80(5) | 1.00(5) | 0.80(5) | | | |
| 22–24 | 0(1) | 0(1) | 1.00(1) | | | | |
| 13 August onward | 0.65(17) | 0.50(16) | 0.94(16) | 0.79(14) | 0.90(10) | 0.71(7) | |

* Values in parentheses are sample sizes.

**Appendix 24**
Measurements of Thick-billed Murres collected at Prince Leopold Island, N.W.T., 1975–77

| Catalog number | Collection date | Wing length, mm | Tarsus length, mm | Culmen, mm | Weight, g | Breeding status |
|---|---|---|---|---|---|---|
| *Males* | | | | | | |
| 75/1 | 8 June 1975 | 213 | — | 38 | 901 | B |
| 2 | 8 | 216 | — | 37 | 943 | B |
| 3 | 8 | 223 | — | 37.5 | 953 | B |
| 4 | 8 | 219 | — | 33.5 | 884 | B |
| 5 | 8 | 214 | — | 31.4 | 946 | B |
| 6 | 8 | 213 | — | 36.2 | 836 | B |
| 11 | 5 July 1975 | 200 | — | 34.4 | 809 | B |
| 13 | 21 | 215 | — | 36.4 | 994 | B |
| 16 | 24 | 208 | — | 36.0 | 949 | B |
| 17 | 24 | 216 | — | 33.9 | 928 | B |
| 18 | 24 | 213 | — | 36.1 | 962 | B |
| 19 | 24 | 209 | — | 34.0 | 908 | B |
| 20 | 11 August 1975 | 215 | — | 36.1 | 909 | B |
| 21 | 11 | 211 | — | 34.0 | 848 | NB |
| 25 | 11 | 220 | — | 33.9 | 961 | B |
| 31 | 12 | 214 | — | 35.9 | 910 | B |
| 33 | 12 | 219 | — | 33.2 | 901 | B |
| 34 | 12 | 208 | — | 32.5 | 891 | B |

**Appendix 24** (cont'd)

| Catalog number | Collection date | Wing length, mm | Tarsus length, mm | Culmen, mm | Weight, g | Breeding status |
|---|---|---|---|---|---|---|
| 76/1 | 23 May 1976 | 219 | — | 38.2 | 979 | (B) |
| 2 | 23 | 220 | — | 34.6 | 1074 | (B) |
| 3 | 23 | 220 | — | 37.3 | 928 | (B) |
| 4 | 23 | 224 | — | 36.0 | 884 | (B) |
| 7 | 23 | 221 | — | 37.0 | 1010 | (B) |
| 8 | 23 | 218 | — | 36.0 | 1006 | (B) |
| 9 | 23 | 219 | — | 35.6 | 902 | (B) |
| 11 | 23 | 214 | — | 32.4 | 915 | (B) |
| 12 | 23 | 225 | — | 36.5 | 965 | (B) |
| 13 | 23 | 218 | — | 35.3 | 929 | (B) |
| 14 | 23 | 220 | — | 40.5 | 935 | (B) |
| 17 | 23 | 218 | — | 36.1 | 975 | (B) |
| 18 | 23 | 218 | — | 34.5 | 1010 | (B) |
| 20 | 23 | 210 | — | 36.1 | 995 | (B) |
| 21 | 4 June 1976 | 227 | — | 35.8 | 1006 | (B) |
| 22 | 4 | 215 | — | 36.2 | 902 | (B) |
| 23 | 4 | 218 | — | 34.6 | 1049 | (B) |
| 25 | 9 July 1976 | 219 | — | 35.0 | 889 | B |
| 30 | 15 | 224 | — | 33.0 | 1033 | B |
| 32 | 15 | 220 | — | 34.8 | 930 | B |
| 33 | 15 | 208 | — | 34.0 | 867 | B |
| 35 | 15 | 229 | — | 40.0 | 857 | B |
| 36 | 15 | 210 | — | 36.1 | 1006 | B |
| 37 | 15 | 216 | — | 36.9 | 822 | (NB) |
| 38 | 15 | 217 | — | 36.6 | 1032 | B |
| 39 | 15 | 216 | — | 33.0 | 974 | B |
| 40 | 15 | 219 | — | 36.2 | 836 | B |
| 41 | 15 | 218 | — | 36.0 | 813 | NB |
| 43 | 15 | 223 | — | 35.9 | 911 | B |
| 64 | 12 August 1976 | 211 | — | 36.5 | 998 | B |
| 68 | 12 | 208 | 34.3 | 33.0 | 802 | B |
| 69 | 12 | 222 | 35.6 | 33.3 | 853 | B |
| 70 | 12 | 225 | 35.8 | 34.1 | 855 | NB |
| 74 | 18 | 205 | — | 33.8 | 917 | B |
| 77/1 | 8 June 1977 | 209 | — | 34.2 | 898 | (B) |
| 2 | 8 | 223 | — | 38.4 | 930 | (B) |
| 3 | 8 | 221 | — | 34.1 | 885 | (B) |
| 5 | 8 | 218 | — | 37.4 | 897 | (B) |
| 6 | 8 | 225 | — | 35.5 | 925 | (B) |
| 7 | 8 | 224 | — | 33.2 | 905 | (B) |
| 8 | 8 | 214 | — | 36.4 | 1017 | (B) |
| 9 | 14 | 215 | — | 35.1 | 850 | B |
| 11 | 14 | 218 | — | 34.9 | 850 | (B) |
| 12 | 14 | 219 | — | 36.2 | 865 | (B) |
| 13 | 18 | 211 | — | 36.9 | 930 | B |
| 14 | 18 | 218 | — | 34.3 | 880 | B |
| 17 | 30 | 215 | — | 37.3 | 920 | B |
| 18 | 30 | 214 | — | 34.3 | 925 | B |
| 19 | 30 | 211 | — | 33.8 | 975 | B |
| 20 | 30 | 209 | 35.5 | 35.5 | 937 | B |
| 22 | 30 | 221 | 36.0 | 33.0 | 929 | NB |
| 23 | 30 | 210 | 37.7 | 33.8 | 916 | B |
| 26 | 30 | — | — | 29.4 | 893 | B |
| 28 | 30 | 212 | — | 32.2 | 973 | NB |
| 29 | 30 | 205 | 38.0 | 35.7 | 1035 | NB |
| 32 | 30 | 215 | 36.4 | 35.5 | 909 | (NB) |
| 33 | 30 | 215 | 37.4 | 34.0 | 851 | B |
| 34 | 30 | 212 | 36.0 | 33.2 | 998 | B |
| 36 | 15 July 1977 | 214 | — | 34.1 | 1023 | B |
| 37 | 15 | 218 | — | 34.1 | 921 | B |
| 38 | 15 | 196 | — | 34.4 | 838 | B |
| 39 | 15 | 209 | — | 32.4 | 852 | NB |
| 40 | 15 | 209 | — | 34.2 | 969 | NB |
| 41 | 15 | 205 | — | 35.0 | 799 | B |
| 47 | 10 August 1977 | 210 | — | 37.4 | 1004 | (NB) |
| 48 | 10 | 209 | — | 32.8 | 850 | NB |
| 49 | 10 | 216 | — | 34.5 | 852 | NB |

**Appendix 24** (cont'd)

| Catalog number | Collection date | Wing length, mm | Tarsus length, mm | Culmen, mm | Weight, g | Breeding status |
|---|---|---|---|---|---|---|
| *Females* | | | | | | |
| 75/7 | 14 June 1975 | 211 | — | 33.5 | 877 | (B) |
| 8 | 14 | 211 | — | 32.0 | 848 | (B) |
| 9 | 14 | 212 | — | 34.8 | 827 | (B) |
| 10 | 14 | 210 | — | 32.5 | 1056 | (B) |
| 12 | 9 July 1975 | 216 | — | 32.0 | 881 | NB |
| 14 | 21 | 216 | — | 36.1 | 843 | NB |
| 15 | 24 | 209 | — | 32.7 | 907 | B |
| 22 | 11 August 1975 | 212 | — | 29.2 | 814 | B |
| 23 | 11 | 210 | — | 35.9 | 863 | B |
| 24 | 11 | 212 | — | 32.6 | 863 | B |
| 26 | 11 | 214 | — | 36.0 | 922 | B |
| 27 | 12 | 213 | — | 33.3 | 875 | B |
| 28 | 12 | 206 | — | 34.5 | 765 | B |
| 29 | 12 | 206 | — | 34.5 | 765 | B |
| 30 | 12 | 213 | — | 30.5 | 858 | B |
| 31 | 12 | 211 | — | 28.6 | 767 | B |
| 35 | 12 | 209 | — | 32.3 | 831 | (NB) |
| 36 | 12 | 208 | — | 32.1 | 936 | B |
| 76/5 | 23 May 1976 | 211 | — | 34.8 | 862 | (B) |
| 6 | 23 | 217 | — | 30.7 | 884 | (B) |
| 10 | 23 | 222 | — | 36.9 | 1009 | (B) |
| 15 | 23 | 215 | — | 31.6 | 982 | (B) |
| 16 | 23 | 223 | — | 35.4 | 1005 | (B) |
| 19 | 23 | 207 | — | 32.8 | 831 | (B) |
| 24 | 9 July 1976 | 224 | — | 32.0 | 889 | B |
| 26 | 9 | 224 | — | 31.6 | 960 | B |
| 27 | 9 | 220 | — | 32.8 | 869 | (NB) |
| 28 | 9 | 217 | — | 34.8 | 881 | B |
| 29 | 15 | 221 | — | 34.1 | 830 | B |
| 31 | 15 | 222 | — | 33.4 | 867 | B |
| 34 | 15 | 228 | — | 33.8 | 734 | B |
| 42 | 15 | 209 | — | 35.6 | 746 | NB |
| 66 | 12 August 1976 | 210 | 36.3 | 34.0 | 851 | B |
| 67 | 12 | 220 | — | 32.3 | 863 | B |
| 71 | 12 | 213 | 35.2 | 31.4 | 869 | B |
| 77/4 | 8 June 1977 | 218 | — | 35.6 | 862 | (B) |
| 10 | 14 | 217 | — | 35.8 | 825 | (B) |
| 15 | 30 | 220 | — | 34.0 | 890 | (NB) |
| 16 | 30 | 220 | — | 36.0 | 930 | B |
| 21 | 30 | 215 | 36.0 | 32.9 | 883 | B |
| 24 | 30 | 218 | 35.5 | 35.7 | 1101 | B |
| 25 | 30 | 211 | 35.5 | 33.9 | 933 | B |
| 27 | 30 | 214 | 35.0 | 30.5 | 1080 | B |
| 30 | 30 | 215 | 34.9 | 31.2 | 995 | B |
| 31 | 30 | 211 | 35.1 | 31.0 | 883 | (NB) |
| 42 | 10 August 1977 | 215 | — | — | 786 | B |
| 43 | 10 | 220 | — | 34.4 | 890 | B |
| 44 | 10 | 211 | — | 34.6 | 840 | B |
| 45 | 10 | 223 | — | 30.2 | 804 | B |
| 46 | 10 | 206 | — | 34.1 | 823 | B |

* *Breeding Status*. B = breeder, NB = non breeder, (B) or (NB) = determination uncertain. The status of each bird was determined by the presence (B), or absence (NB) of a fully developed brood-patch. Letters in parentheses indicate an uncertain determination. All adults collected before 10 June were considered breeders because, although at this stage brood-patches had not yet developed, there was other evidence to suggest that all birds present at the colony prior to this date were breeders. Birds with incomplete brood-patches during the period 25 June – 15 July were considered to be non-breeders, but given a classification of determination uncertain: (NB).

## Appendix 25

Details of food organisms identified in the digestive tract of Thick-billed Murres collected at Prince Leopold Island in 1976

| Prey taxon | Specimen no. of murre | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 4 | 6 | 7 | 8 | 9 | 11 | 12 | 13 | 21 | 22 | 24 | 25 | 26 | 27 | 28 | 30 | 32 | 33 | 38 | 39 | 41 | 42 | 43 | 65 | 67 | 69 | 74 |
| *Boreogadus saida* | 3 | 1 | 2 | 4 | 1 | 6 | 3 | 4 | 2 | 3 | 1 | 1 | 1 | 4 | — | 15 | 1 | 1 | 7 | — | 1 | 2 | 2 | 4 | 5 | 3 | ? |
| *Triglops* spp. | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — |
| Unidentified fish | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | — | — | — | — | — | — | — | — | — | — | — | — |
| *Parathemisto* spp. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | — | — |
| *Onisimus* spp. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — |
| Unident. crustacea | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | ? |

## Appendix 26

Details of food organisms identified in the digestive tract of birds collected at Prince Leopold Island in 1977

| Prey taxon | Specimen no. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 7 | 9 | 10 | 12 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 34 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 |
| *Boreogadus saida* | 1 | 9 | 5 | 3 | 2 | 13 | — | — | 5 | 6 | 10 | 3 | 3 | 11 | 3 | 4 | 2 | 4 | 9 | 3 | 1 | 7 | 4 | 4 | 2 | 1 | 3 | — | 1 | 1 | 6 | 1 | 1 | 2 | 3 | 1 |
| *Triglops* spp. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Unidentified fish | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Parathemisto libellula* | — | — | — | — | — | 1 | — | — | — | — | — | — | — | 6 | — | — | — | — | — | — | — | — | 16 | — | — | — | — | — | — | — | — | — | — | 7 | — | — |
| *Parathemisto* spp. | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 17 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — |
| *Mysis oculata* | — | — | — | — | — | — | 1 | 5 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Gammarus setosus* | — | — | — | — | — | — | 15 | 62 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *G. wilkitzkii* | — | — | — | — | — | — | 1 | 3 | — | 1 | — | 2 | 1 | — | — | — | — | — | — | — | — | — | 5 | — | — | — | — | — | — | 8 | — | — | — | 1 | — | — |
| *Gammarus* spp. | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Gamarellus homari* | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Onisimus littoralis* | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Onisimus* spp. | — | — | — | — | — | — | 8 | 6 | — | 1 | — | 1 | — | — | — | — | — | — | — | — | — | — | 113 | — | — | — | — | — | — | 27 | — | — | — | 3 | — | — |
| *Weyprechtia pinguis* | — | — | — | — | — | — | 36 | 113 | — | — | — | 3 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Parapleustes bicuspis* | — | — | — | — | — | — | 1 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Pontogenia inermis* | — | — | — | — | — | — | 17 | 114 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Apherusa glacialis* | — | — | — | — | — | — | 11 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Anonyx sarsi* | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Monoculodes* spp. | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Unidentified crustacea | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Squid (*Gonatus fabricii*?) | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — |

## Appendix 27

## Derivation of the formula relating the minimum density ratio to differences in foraging distance between different feeding areas

Given the choice between two feeding areas, at distances $L_1$ and $L_2$ from the colony, with $L_1 < L_2$, what ratio of prey densities ($D_1$, $D_2$) makes the two alternatives equally profitable? If the total time available for foraging per day is fixed, then:

$$T_1 + t_1 = T_2 + t_2 \qquad [1]$$

where $T$ is travel time to the feeding area and $t$ is fishing time.

Assuming that fishing time* is inversely proportional to (prey density)$^{1/3}$ then:

$$t_2 = t_1 (D_1/D_2)^{1/3}$$

Hence substituting in eq. [1]:

$$T_1 + t_1 = T_2 + t_1 (D_1/D_2)^{1/3} \qquad [2]$$

And assuming that murres travel to their feeding area in a straight line:

$$T = 2VL/s$$

where $V$ = the number of visits to the colony per day by members of a pair and $s$ = the flight speed.

Substituting in eq. [2]:

$$2VL_1/s + t_1 = 2VL_2/s + t_1 (D_1/D_2)^{1/3} \qquad [3]$$

Rearranging equation [3] gives:

$$\frac{D_2}{D_1} = \left( \frac{t_1}{t_1 + \left[ \frac{2VL_1 - 2VL_2}{s} \right]} \right) \qquad [4]$$

---

* The assumption that fishing time is inversely proportional to the cube root of prey density is based on the relationship between density and minimum distance to the nearest prey object. The assumption should be true in circumstances where the bird can see its next capture from the position at which it takes its last. If there is an intermediate searching period before the next prey object is located and pursuit begins, then the power relationship will be altered, as frequency with which prey is located is proportional to linear distance travelled. Judging from the number of prey items estimated to be taken by an adult murre in the course of a foraging trip, it seems likely that many of the intervals between captures are sufficiently brief to warrant the assumption, but in reality a hybrid model, incorporating components of searching time and pursuit time, would probably be more appropriate.

## Appendix 28

### Derivation of equation [7] relating mean density of prey to colony size

Assumptions:

1. The colony is situated on an island of negligible area.
2. Sea extends to infinity in all directions.
3. A colony of one pair occurs where prey density is just sufficient to allow the rearing of a chick, using the maximum amount of foraging time available. This density ($D_1$) is designated as unity.
4. At the minimum density ($D_1$) the pair requires an area $a_1$ for foraging.
5. Feeding time is inversely proportional to the cube root of prey density (App. 27, footnote*).
6. Each adult has a maximum of 10 h daily available for foraging.
7. The area necessary for one pair to forage ($a$) is inversely proportional to the square root of prey density.
   Let $D_x$ be any density of prey greater than $D_1$

From assumption 5:

$$t_1/t_x = (D_x/D_1)^{1/3}$$

From assumption 3 and 6:

$$D_1 = 1, t_1 = 20\text{ h}$$

Hence at $D_x$

$$t_x = t_1 \cdot (D_I/D_x)^{1/3} = 20/(D_x)^{1/3}$$

From assumption 6:

$$T_x = 20 - t_x = 20\,[1 - 1/(D_x)^{1/3}] \qquad [1]$$

$$\text{total distance flown} = ST_x$$

Hence foraging radius = Distance flown/2$V$ = $ST_x/2V$
Substituting eq. [1],

$$\text{foraging radius} = \frac{20S}{2V}\left[1 - \frac{1}{(D_x)^{1/3}}\right] \qquad [2]$$

Hence total foraging area =

$$\pi(\text{foraging radius})^2 = \pi\left\{\frac{20S}{2V}\left[1 - \frac{1}{(D_x)^{1/3}}\right]\right\}^2 \qquad [3]$$

From assumption 7:

$$a_1/a_x = (D_x/D_1)^{1/2}$$

Hence $a_x = a_I\,(D_1/D_x)^{1/2} = a_1/(D_x)^{1/2}$ [4]

Total colony size ($N$) = Foraging area of colony/area required by one pair

Hence, combining eqs. [3] and [4]:

$$N = \pi\left\{\frac{20S}{2V}\left[1 - \frac{1}{(D_x)^{1/3}}\right]\right\}^2 \cdot \frac{(Dx)^{1/2}}{a_1} \qquad [5]$$

# Other Publications in the Monograph Series

1. The Murres: their distribution, populations and biology, — a study of the genus *Uria*. By Leslie M. Tuck. Cat. No. R66-2161.1, price $2.50, publ. 1960. Out of print.
2. Muskoxen in Canada, a biological and taxonomic review. By John S. Tener. Cat. No. R65-7/2, price $3.25, publ. 1965. Out of print.
3. The migratory barren-ground caribou of Canada. By John P. Kelsall. Cat. No. R65-7/3, price $3.55, publ. 1968. Out of print.
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